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FOREST *Science*

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Biology and Control of the White-Fir Sawfly

BY
GEORGE R. STRUBLE

SAWFLIES have been collected on true firs since 1910, but until recent years they caused no more than minor damage. In 1951 and 1952, however, sawfly outbreaks were reported in white fir (*Abies concolor* (Gord. and Glend.) Lindl.) on the Plumas National Forest, near La Porte, Plumas County, Calif. By 1954, second-growth white fir timber on nearly 10,000 acres was infested in varying degrees of intensity. Other outbreak areas, ranging in size from a few hundred to several thousand acres, were reported in 1953 and 1954 from the North Warner Mountains in Modoc County to the southern part of the Sierra Nevada in Fresno County. These outbreaks occurred in both old and young fir stands. One of the largest was in Yosemite National Park, Mariposa County.

The species responsible for these outbreaks was the white-fir sawfly, designated *Neodiprion abietis* complex by Ross.[1] It has long been considered a minor pest of white fir and red fir (*Abies magnifica* A. Murr.).

Research work was begun in 1952 to determine the habits of the white-fir sawfly, its importance as a forest pest, and methods of control. Beginning with the flight and oviposition period in the fall of 1952, the studies were continued through one complete generation to emergence the next fall, 1953. Additional data were collected in 1954 and 1955.

Occurrence and Symptoms of Outbreaks

Epidemic populations of the white-fir sawfly occur in rather dense, contiguous bodies of timber in which the predominant species is true fir. Second-growth stands, mostly of white fir between 60 and 80 years old, are most severely infested (Fig. 1). In old-growth timber the infestations are confined more to the understory. Tree species other than true fir occurring in admixture do not

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The author is Entomologist at the California Forest and Range Experiment Station, Forest Service, U. S. Dept. of Agric., Berkeley, Calif. Forest Entomologists R. L. Lyon, M. M. Furniss, C. B. Eaton, and R. C. Hall of the Station assisted in the investigations. Dr. C. G. Thompson, Dr. E. A. Steinhaus, and Dr. E. C. Clark of the Department of Biological Control, University of California, cooperated in the identification and evaluation of a virus disease. Dr. C. G. Thompson and the Forest Insect and Disease Laboratory, Northeastern Forest Experiment Station, Forest Service, U. S. Department of Agriculture, New Haven, Conn., cooperated in the virus inoculation experiments. Dr. Robert Lambert, Division of Forest Biology, Canada Department of Agriculture, and Dr. H. H. Ross, Illinois Natural History Survey, identified the white-fir sawfly.

[1]Ross, Herbert H. 1955. The taxonomy and evolution of the sawfly genus Neodiprion. For. Sci. 1:196-209.

become infested. Often, infestations are found in dense stands of young saplings and poles. In general, defoliation is most pronounced in understory trees and in the lower parts of crowns of all trees. Occassionally, 80 to 90 percent of the foliage of second-growth white fir dominants is destroyed. Open bodies of timber are relatively free from infestation.

Active infestations may be detected readily by the fading, yellowish-brown remnants of 1-year or older foliage fed upon by the larvae. After about 3 weeks, affected crowns present a lacelike silhouette, with only the midribs of needles remaining. These remnants dry out and drop away within 2 to 3 months, new terminal foliage grows, and the trees improve in appearance.

Effect of Defoliation

The damage caused by defoliation in white fir stands was considered early in this study. Many of the white firs in affected areas were almost completely defoliated. Tree mortality seemed possible. Trees weakened by loss of foliage were considered subject to infestation by tree-killing bark beetles and borers. It seemed likely, too, that reduction in growth after defoliation would be an additional drain on forest production. In stands of young saplings the effect on Christmas tree values was studied.

In 1954, three years after outbreaks had begun, an appraisal of losses as a direct result of defoliation was made. At the same time, investigations were made to determine whether bark beetles and borers were present. This was done in 10 randomly selected plots representing a good cross section of affected forests of true fir. Each plot contained 100 trees; a total of 1,000 trees were examined.

The results of this appraisal showed: (1) that mortality was somewhat less than 1 percent of the number of trees examined; (2) that mortality was confined to intermediate and suppressed trees; and (3) that there was no evidence of bark beetles or borers in the defoliated trees.

15654–A

FIGURE 1. *Dominant and codominant second-growth white-fir defoliated by fir sawfly in 1952.*

The effect of defoliation on growth was determined from increment cores obtained from 21 dominant and codominant trees on which 65 percent or more of the foliage was destroyed by sawflies during the outbreak period. Cores obtained after the completion of the 1954 growth revealed a reduction in increment of 58 percent below that of 1950, one year before the outbreak. Cores obtained in the spring of 1956, with an additional year's growth, revealed that current annual increment was reduced to less than one-third of the average annual increment for the 10-year period preceding the outbreak (Fig. 2). Reductions in increment followed immediately after the onset of the outbreak, and there was little evidence of recovery 2 years after the epidemic ended.

Defoliation in a single area of sapling white fir and red fir caused extensive damage to potential Christmas trees. Complete recovery of foliage following this outbreak may require 5 to 7 years.

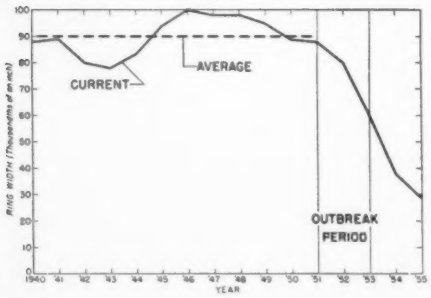

FIGURE 2. *Current annual increment before, during, and after white-fir sawfly outbreak.*

Life Stages

Adult

The male sawflies (Fig. 3) are 5 to 6 mm. long, with 21-segmented, pectinate antennae. The color of antennae, head, thorax, and abdomen is dark brown; mouth parts, legs, and tarsi are light yellowish brown.

The females are 6 to 8 mm. long, with serrate, 21-segmented antennae. The color of antennae, compound eyes, ocelli, and mandibles is dark brown to black. On each side of the scutum is a large, lateral, dark brown bar. Remaining portions of the head, thorax, and appendages are light yellowish brown. The abdomen is turquoise or light yellowish brown, depending on distension and maturation of eggs.

Eggs

The color of the egg is turquoise, and the chorion surface is slightly wrinkled from the time of deposition in late fall until the beginning of embryo development in spring. The eggs become greatly swollen, smooth, and light gray or off white before the larvae hatch. They are cigar shaped dorsally and crescent shaped laterally. The length is 1½ mm. and width 1/3 mm.

Larva

The larva passes through 6 instars before pupation. All except the last instar have olive-green bodies and black heads. The color of the body changes from darker to lighter shades of olive green during development, from the first through the fifth instar. In the sixth or prepupal instar the larva has a cream-colored head with black ocelli and dark-brown mouth parts, and a yellowish-green, longitudinally striped body. A median dorsal line is characteristic among third instar larvae; two lateral lines occur among the fourth and fifth instar larvae and broaden among sixth instar larvae. The approximate size and duration of each instar is as follows: First, 3 to 5 mm., 5 days; second, 6 to 8 mm., 5 days; third, 10 to 13 mm., 4 days; fourth, 16 to 20 mm., 4 days; fifth, 25 to 29 mm., 6 days; sixth or prepupal instar, 20 to 25 mm.

Cocoon

The cocoon formed by the prepupal larva is a tough, fibrous, cylindrical case with rounded ends, varies in length from 5 to 8 mm., and is about 3 mm. wide. Its color at first is silver, and it turns to golden brown after 10 days to 2 weeks. Most often, cocoons are found within the soil immediately below the duff; occasionally they occur on the duff surface; infrequently they are attached to green foliage.

Seasonal History

Adult flight and mating

Emergence of adults, flight, mating, and oviposition occur in late fall, usually between October 20 and November 5. In 1952, these events took place from October 23 to November 3; in 1953, they occurred 10 days later; in 1954, from October 20 to November 1. Such differences were traceable directly to seasonal temperature variations.

After the adults emerge from the cocoons, they may remain within the soil or duff, or migrate to the surface and take flight promptly, depending on soil temperatures. Warm weather in late October 1952 stimulated so many adults to emerge in heavily infested areas during the day that their activity was audible. In 1953, although a good many adults had emerged from cocoons by the end of October, very few were in flight. Most of them remained

within the duff and soil. The next year adults were in flight again by October 20.

Limited information on the sex ratio indicated that the proportion of males and females is about equal. The males emerge in greater numbers during the first few days of the flight period, whereas more females than males emerge later on.

Mating was not observed, but evidence indicated that this function is accomplished before and during the oviposition period. Males were observed to hover in the immediate vicinity of females crawling over foliage and near other females in the act of oviposition. Both males and females are most numerous and active among the host tree crowns during the day, from about 10:00 a. m. to 6:00 p. m.

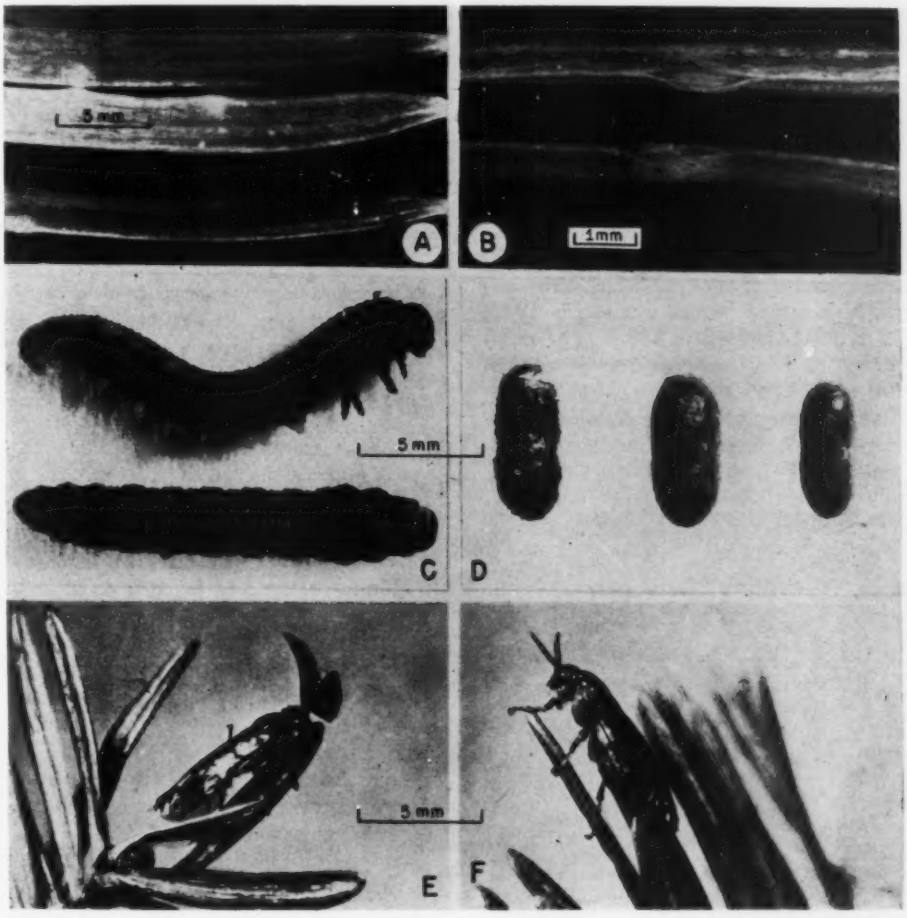

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FIGURE 3. *Life stages of the white-fir sawfly: (A) Swellings on edges of needles indicate eggs, (B) swollen eggs in needle edges just prior to hatching, (C) larvae, (D) cocoons, (E) adult male, and (F) adult female.*

Oviposition

Eggs are deposited by the female sawfly along the edges of the white fir needles in slits cut through the cuticle. As a general rule, one egg is deposited in each needle. In fact, only about 5 percent of all needles examined had 2 eggs per needle; as many as 3 and 4 eggs in a needle was rare. Needles containing freshly deposited eggs are slightly swollen on their edges where the eggs are inserted. These swellings turn off-green to yellowish by the time eggs hatch in the spring.

The female oviposits in each successive needle, often laying more than 60 eggs before leaving a branchlet. Information on the number of eggs that may be deposited by a single female was gained from dissections of 10 gravid females. The average number of fully developed eggs per female was 67; the range was 53 to 83. The average number of eggs per 6-inch twig containing about 15 laterals was 160 in 1953, 40 in 1954, and 42 in 1955. The number varied from less than 6 to more than 450.

Although eggs may be deposited in 4-year-old foliage, younger needles are preferred for oviposition. Among 4,520 eggs recorded in early June, 1953, before the opening of current growth buds, 68 percent were in the 1952 foliage, 26 percent in the foliage of the previous year, 5 percent in the third year's foliage, and 1 percent in the fourth year's foliage.

The eggs are laid during the last two weeks in October and remain in an undeveloped stage in the foliage through the winter and most of the spring. Hatching occurs from mid-May to mid-June, or just before or during the period when current growth buds of white fir are breaking. Prolonged cold in the spring of 1953 delayed hatching until June; in 1954 and 1955, hatching began around the middle of May; in 1956, it did not occur until June.

15735–J

FIGURE 4. *Feeding group of third instar larvae in white fir foliage.*

Development of larvae

After hatching from eggs deposited in a given location in the needles of one or more twig ends, the young larvae tend to gather and feed gregariously on these needles or on nearby foliage. As a result, the group of larvae from an initial clutch of eggs is termed a colony. In a given colony, each needle may contain from 2 to many individuals. In feeding, the larvae orient themselves with their heads toward the apex of the needle (Fig. 4). They continue to feed in this position through the fifth instar. Frequently, more than 20 first- and second-instar larvae feed together on a single needle. In the fourth and fifth instars, the number is usually about 10 larvae per needle. Colonies of larvae vary in number from somewhat less than 30 to more than 100 individuals.

In the spring the larvae feed at first on the previous year's foliage. Feeding continues progressively into the older foliage for the full period of larval development. This results in the destruction of leaf tissue in varying amounts. Where feeding is intensive, all except the midrib of each needle is consumed. The larvae seldom feed on the current year's foliage.

The rapid development and heavy feeding of larvae result in great quantities of

frass, which accumulates on the forest floor. In 1953, weekly frass deposits were measured on a square yard of muslin cloth for the first, second, and third larval instars. Quantities collected were 1.2 cc., 38.3 cc., and 220.8 cc. respectively. These deposits all originated from undisturbed populations of larvae established initially in the lowest branches directly above the muslin square.

Disturbances caused by wind movement or the sudden jarring of trees or branches on which larvae are feeding result in varying behavior among different-aged larvae. The younger larvae, including first to third instars, remain attached to the needles, swaying the fore parts of their bodies to and fro. The older ones release their holds on the foliage and drop to the branches below or to the ground. A severe gust of wind often covers the ground with larvae. Later these larvae migrate back toward the crown by crawling up the trunk of the tree. This habit tends to increase the amount of defoliation as well as the size of colonies in the lower limbs of the larger trees and the entire crowns of understory host trees. At larval maturity and during cocooning, the extent of the defoliation of the older foliage is not readily seen because the current foliage is about two-thirds grown.

Sixth-instar larvae are rarely found among maturing colonies because many of the mature fifth-instar larvae and most of the sixth-instar larvae drop to the ground. Very few of either stages may be seen migrating downward. The sixth-instar larvae enter the soil layer just beneath the duff and form cocoons.

The prepupal stage within the cocoon remains quiescent for varying periods of diapause before pupation. Prepupae that mature to adults in late October pupate within 45 to 70 days; those that go into an extended diapause may remain quiescent for 400 days before pupation. The percentage of prepupal larvae that develops to the adult stage in one season has not been determined. However, there is considerable evidence to indicate that only a small minority remains in an extended diapause.

The life history, shown in Figure 5, reveals, in general, a single generation of the sawfly each year.

Biological Control Factors

Insect enemies

The white-fir sawfly is attacked by numerous insects, mostly parasites. Some of its enemies, however, are predators, and a few of these are active as both larvae and adults. Most of the insect enemies attack the sawfly larvae; only a single species has been found to attack eggs. Some soil-inhabiting insects attack the prepupal larvae in-

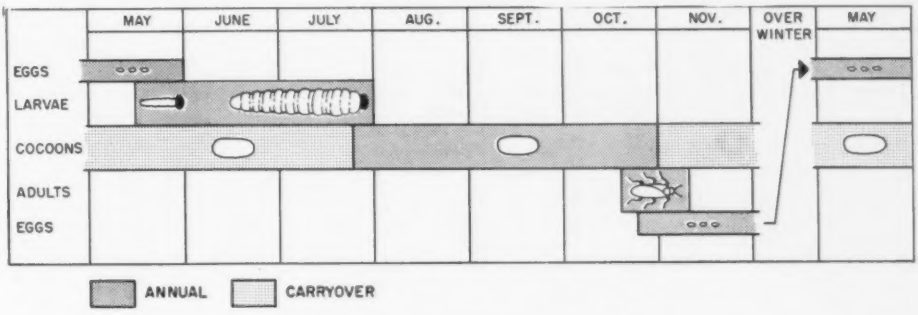

FIGURE 5. *Life cycle of white-fir sawfly.*

side cocoons. The importance of these insect enemies in controlling the sawfly was not determined. Much was learned, however, about the kinds of insects and the different sawfly stages affected (Table 1).

Disease

The possible occurrence of a native virus epizootic among outbreak populations of the white-fir sawfly was a primary consideration in this study. Experience with native infections in outbreaks of other sawfly species in the East has demonstrated that diseases can quickly control infestations of sawflies. Therefore, a constant lookout was kept for evidences of infection of white-fir sawfly.

In addition, water suspensions of the virus that attacks the European pine sawfly, *Neodiprion sertifer* (Geoff.), in the East, were sprayed on white fir sawfly larvae in the third and fourth instars to determine whether the species is susceptible to this virus. None of the sprayed larvae exhibited signs of virus infection. This was not entirely unexpected inasmuch as insect viruses usually are highly host specific.

Suddenly, in mid-July 1953, a native polyhedral virus epizootic appeared among the fourth- and fifth-instar larvae. Collections of larvae made within 7 days of the discovery of the epizootic were examined by Dr. E. A. Steinhaus and Dr. C. G. Thompson of the University of California, and were found to be about 50 percent infected. Examination of collections made 15 days later showed that more than 90 percent of the populations in all areas studied were infected, regardless of population density. Other infections occurred simultaneously among sawfly larvae in an outbreak 160 miles distant.

Each year since 1953, the larval populations have been progressively less in study

TABLE 1. Insect enemies[1] of the white-fir sawfly.

Stage attacked	Order	Family	Species	Frequency
			PREDATORS	
Larvae	Hemiptera	Nabidae	*Nabis alternatus* Parsh.	Occasional
	Coleoptera	Melyridae	Undetermined	Occasional
		Cantharidae	Undetermined	Occasional
		Coccinellidae	*Anatus rathvoni* Lec.	Very common
		Coccinellidae	*Neomysia subvittata* (Muls.)	Common
	Diptera	Larvaevoridae	*Phorocera* sp. nr. *hamata* A & W	Common
		Bombyliidae	Undetermined	Occasional
Cocoons	Orthoptera	Stenopelmatidae	*Stenopelmatus longispinus* Brunner	Occasional
	Diptera	Dolichopodidae	Unidentified	Common
	Neuroptera	Raphididae	Unidentified	Common
			PARASITES	
Eggs	Hymenoptera	Eulophidae	*Derestenus* sp.	Rare
Larvae	Hymenoptera	Ichneumonidae	*Exenterus tsugae* Cush.	Common
			Lamachus sp.	Common
			Bathytrix areolatis (Cush.)	Occasional
			Bathytrix sp.	Occasional
			Opidinus sp. nr. *tsugae* (Cush.)	Common
			Endasys subclavatus (Say)	Occasional
			Ischnus sp. nr. *oregonensis* (Cush.)	Common
			Trychosis sp.	Occasional
			Gelis sp.	Occasional
		Pteromalidae	*Tritneptis klugii* (Ratz.)	Very common
		Cleptidae	*Cleptes purpurata* Cr.	Occasional

[1]Determined by specialists in the U. S. National Museum: R. H. Arnet, B. O. Banks, E. A. Chapn, K. V. Krombeim, C. F. W. Muesebeck, R. I. Sailer, L. M. Walkley, L. H. Weld, and W. W. Wirth.

areas. In 1954, and again in 1955, native virus infections were found among larvae after the fourth and fifth instars. Egg counts in 1956 were the lowest since studies were begun; they were about 1 percent of the number found in 1953.

Larvae infected by this virus become limp and flaccid, their color changes to dirty brownish gray, and within a few days they shrivel considerably. They cease feeding and reverse their normal orientation on the needles, with their heads pointed toward the needle base rather than the apex. Evidence of infection has never been observed among first- and second-instar larvae and was rare among third-instar larvae. Among dissected sixth-instar larvae in cocoons, the incidence of infection was 54 percent.

Direct Control Methods

The need for direct suppression methods to reduce white-fir sawfly damage depends in large measure on the duration of infestations and the amount of control exerted by natural factors. In view of the effectiveness of control by a native virus epizootic in the 1953 outbreak and the prevalence of native insect enemies, it is evident that direct control may not always be necessary.

A direct control method that was tried in 1953, however, clearly demonstrates that the sawfly can be controlled with DDT sprays applied by aircraft. The spray formulation and timing of the application were based largely on control experience with sawflies in the East.[2] An 80-acre plot was treated at the rate of 1 pound of DDT in 1 gallon of fuel oil per acre. The spray was applied as soon as possible after the larvae hatched. Between 95 and 100 percent of the larvae were killed in the treated area, while on a comparable area that was not sprayed little or no mortality occurred. The spraying cost $0.90 per acre. The aircraft, a Nordyne high-wing monoplane equipped with rotary-brush spray dispersers, was flown at about 100 feet above the treetops. An even higher degree of control at much less cost for materials may be possible with an aerial spray application of a water suspension of the native virus if control should ever become necessary.

[2]Benjamin, Daniel M. 1955. The biology and ecology of the redheaded pine sawfly. U. S. Dept. Agric. Tech. Bull. 1118, 57 pp., illus.

Summary

An outbreak of the white-fir sawfly occurred from 1951 to 1955 in stands of white fir in California. Before it subsided it resulted in drastic growth reduction of heavily defoliated trees and in some killing of suppressed trees.

The white-fir sawfly has a predominant 1-year cycle, with a fraction of each generation carrying over a second year. Mating and oviposition occur during the last 2 weeks of October. Eggs are laid under the epidermis along the edges of needles. They hatch between May 15 and June 15. The larvae pass through 5 feeding instars, all on the older foliage, Larvae of the sixth or prepupal instar migrate and spin cocoons in the duff or soil between July 20 and 25. Most of these larvae pupate and develop to adults by late October. A small percentage of them, however, remain in this stage over winter, and are believed to mature in October of the second year.

An evaluation of damage following defoliation revealed minor killing among suppressed trees and drastic growth reduction in all affected stands.

A native epizootic polyhedral virus caused dramatic reductions in sawfly populations in 1953 and subsequent years. Infections showed up in the fourth and fifth instars. Several species of native parasites and predators were found, but their control effectiveness was not determined. Control by aerial DDT sprays was highly effective.

Comparative Decay Resistance of Some Common Pines, Hemlock, Spruce, and True Fir

BY
JOE W. CLARK

EARLY WORK AND MOST of the more recent investigations of natural decay resistance have been primarily aimed at finding or comparing the more resistant wood species. Some workers have included moderately resistant and nonresistant species in laboratory tests, but because of sample limitations or differences in technique, their results are difficult to combine into a broad comparison of species. The same is largely true for the results of field tests with stakes and posts of woods of moderate to low decay resistance.

The tests described here were designed to provide more informatiton about decay resistance of common species. Of particular interest was the comparative resistance of commercially prominent pines. Several other coniferous woods were also tested because in certain connections their decay resistance may become a point in question.

Sampling Procedure

Heartwood for testing was collected mainly as sawn lumber at sawmills and retail yards. Most samples were of nominal 1-inch stock. Approximately 20 individuals from private industry, forestry colleges, and the U. S. Forest Service cooperated in collecting the material. The collectors tried to avoid getting more than one sample from a single tree, but it was impossible to determine the position in the tree from which a sample was taken, except that it was from the heartwood. Therefore, the samples may be considered to have come from different trees in most cases and to be reasonably representative of the merchantable heartwood material being manufactured into lumber. Table 1 shows the species used in the test, the number of samples of each species, and the number of collection sources for each species.

The identity of doubtful species, such as hemlock versus true fir, was checked microscopically. For those species having poorly defined sapwood, appropriate chemical indicators (Canadian Dept. of Mines and Resources, 1948; U. S. Forest Products Laboratory, 1948) were used to distinguish heartwood from sapwood.

Blocks for the decay exposures, $1\frac{3}{16}$ by $\frac{5}{8}$ by $\frac{3}{8}$ inches (grain direction), were sawed from the outermost heartwood of each sample. All were free of sapwood, pitch pockets, knots or other abnormalities.

Tests

The soil-block technique (Duncan, 1953) was used in testing the materials for decay resistance. Six-ounce French-square bottles were half filled with fertile topsoil having an adjusted moisture content of 47 percent. A $1\frac{1}{2}$ by 1 by $\frac{1}{4}$-inch ponderosa pine

The author is Pathologist, Forest Products Laboratory, Forest Service, U. S. Department of Agriculture. The Laboratory is maintained at Madison, Wisconsin, in cooperation with the University of Wisconsin.

TABLE 1. Wood samples collected for decay tests with Poria monticola, Lenzites sepiaria, *and* L. trabea.

Species	Number of samples	Collection sources	
		Number	Number of states represented
Eastern white pine (*Pinus strobus*)	25	3	2
Jack pine (*Pinus banksiana*)	20	2	2
Loblolly pine (*Pinus taeda*)	29	2	2
Lodgepole pine (*Pinus contorta*)	28	2	2
Longleaf pine (*Pinus palustris*)	29	2	2
Ponderosa pine (*Pinus ponderosa*)	35	11	5
Red pine (*Pinus resinosa*)	35	3	2
Sugar pine (*Pinus lambertiana*)	34	9	2
Western white pine (*Pinus monticola*)	20	3	2
Noble fir (*Abies procera*)	9	1	1
White fir (*Abies concolor*)	32	3	2
True fir (*Abies* sp.)[1]	16	3	3
Western hemlock (*Tsuga heterophylla*)	14	2	1
Engelmann spruce (*Picea engelmanni*)	20	1	1

[1]Sixteen samples of unidentified true fir were received These were included in the test to increase the sample of true firs.

sapwood feeder block was laid flat on the soil surface in each bottle and the units steam sterilized. After cooling, the feeder block in each bottle was inoculated with a single test fungus. Three weeks later the test blocks were steam sterilized at 212° F. and placed, one to a bottle, on the fungus-covered feeder blocks. The test units were then held 3 months in an incubation room equipped to maintain conditions of 70 percent relative humidity and 80° F.

Before exposure, the blocks were conditioned to 12 percent moisture content and weighed. After exposure, the blocks were removed from the test bottles, air-dried, and again conditioned to 12 percent moisture content and weighed. The percent weight loss for each block was taken as the measure of decay. The sample average for each set of three replicate blocks exposed to a given test fungus was determined, and from these averages the wood species average weight loss for each test fungus was calculated.

Three test fungi were used: *Poria monticola* (Madison 698), *Lenzites sepiaria*[1] (Madison 604), and *L. trabea* (Madison 617). *P. monticola* has been used widely for many years as a general-purpose test fungus, and has often been isolated from decaying wood products such as posts, poles, boats, and decay in wood structures generally, including buildings and bridges. It has not been commonly isolated in the Southern States, however. It occurs in both soil-contacting and above-ground members, but because of the general vigor of its attack, it may be particularly useful for indicating the relative decay resistance of woods exposed to the comparatively severe decay hazard imposed by ground contact.

Lenzites sepiaria is one of the most frequently encountered fungi causing decay of above-ground coniferous woods in all parts of the country, particularly in the South. It occurs commonly in the tops of posts and poles, bridge railings, siding, and

[1]Common usage favors this spelling in preference to the approved "*saepiaria.*"

exterior trim, where rain seepage creates a decay hazard. High temperature tolerance and the capacity to withstand rather long periods of drying make this fungus adaptable to above-ground exposures.

Lenzites trabea, another frequently used test fungus, occurs commonly above ground in wood exposed to relatively high temperatures and intermittent wetting and drying such as siding, millwork, exposed porches, and bridges. This species is more common in the Northern States than in the South.

Results

The average percent weight losses, from decay in individual samples, each presumably representing a different tree, are shown by the plotted points in Figure 1. The average percent weight losses for the wood species are shown by the bar graphs.

The distribution of plotted points in the figure shows that some species contain trees varying widely in resistance, but other species have trees with a very narrow range of resistance. This is true with respect to resistance to all three test fungi. Therefore, a practical characterization of some of the species requires information about the variation in decay resistance as well as the average resistance.

To consider the variation in resistance from a more utilitarian point of view, it was helpful to observe the proportions of samples (trees) in different resistance classes. Table 2 was prepared for this purpose. Definition of the classes shown in the table is according to weight-loss criteria developed and used in previous testing of natural decay resistance (Moses, 1955; Scheffer and Duncan, 1947; Wangaard *et al.*, 1955), and which so far seem to agree reasonably well with the reputations of the tested woods for durability. These criteria, which follow, were developed from tests in which sample blocks of low decay resistance, such as pine sapwood, lost approximately 60 percent in weight during 3-month exposures to pure cultures of fungi.

Resistance class:	*Average percent weight loss*
Very resistant	0–10
Resistant	11–24
Moderately resistant	25–44
Nonresistant	45+

Table 2 shows that the majority of samples incurred weight losses of 25 percent or more when attacked by any of the three test fungi. By the present rating scheme they would be classed as nonresistant or only moderately decay resistant. These results agreed with the common reputation of the woods for low to moderate resistance. Nevertheless, a considerable portion of samples (or trees) of several pine species showed surprisingly high levels of resistance. For example, wood that was resistant or very resistant (weight losses less than 25 percent) to decay by *Poria monticola*, the most destructive of the test fungi, appeared in 3 to 12 percent of the longleaf, eastern white, loblolly, and ponderosa pine samples. Corresponding figures for the same woods decayed by *Lenzites sepiaria* and *L. trabea* were respectively 41 to 69 and 48 to 74 percent. Samples of three additional species were resistant or very resistant to the latter two fungi—but not to *P. monticola* — namely, the sugar, jack, and red pines; the corresponding percentage figures in these cases were 5 to 18 and 15 to 37.

Comparatively few of the lodgepole pine or western white pine samples, and none of the spruce and fir samples, were as much as moderately resistant (25 to 44 percent weight loss) to any of the fungi. In these woods of lowest resistance, the variation in amounts of decay was strikingly small.

None of the pines was sufficiently resistant to *Poria monticola* to indicate that it might be suitable without preservative treatment for service in ground contact or under other conditions of high decay hazard. Nevertheless, the differences in resistance to this and to the other two test fungi appear large enough to make it worthwhile, where it is practicable to do so, to make some selection among the species for cer-

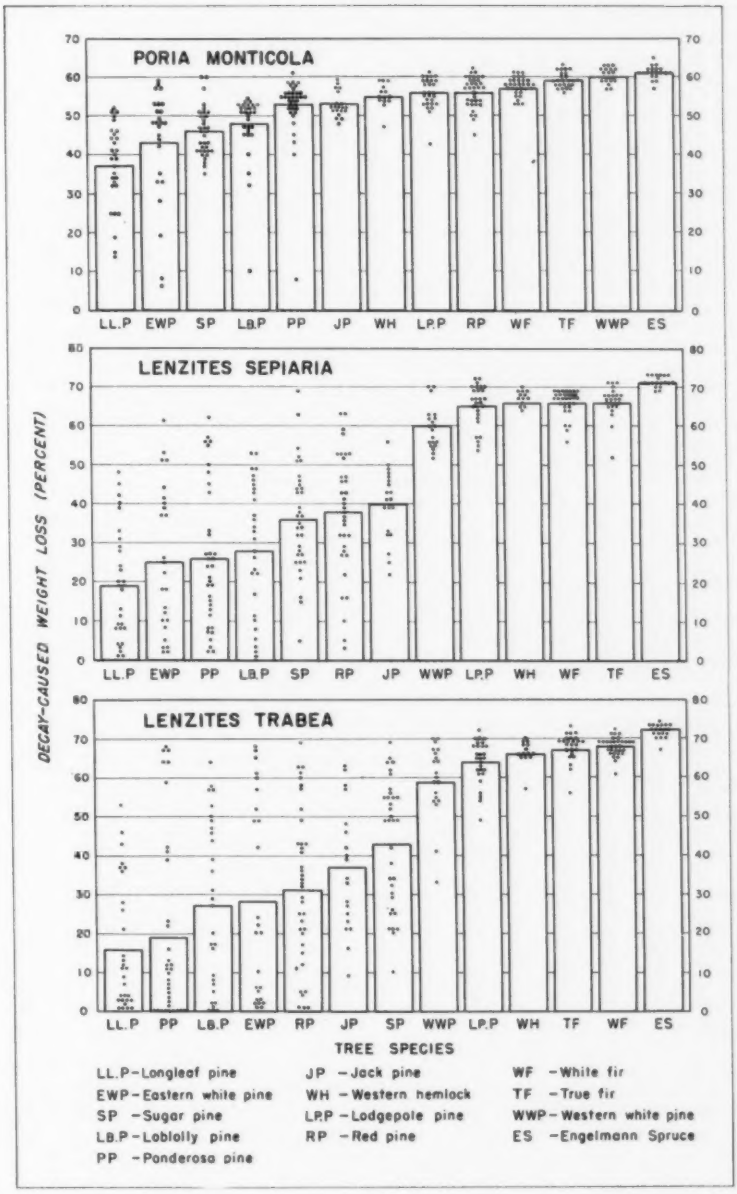

FIGURE 1. *Weight losses in decay-resistance test of specified woods exposed to the indicated test fungi. The plotted points show weight losses of presumably different trees; the bars show average weight losses for the wood species.*

TABLE 2. Distribution of samples according to weight losses incurred in decay tests with the indicated fungi.

Species[1]	Number of samples	Decay by *Poria monticola*— percent weight loss and resistance class				Decay by *Lenzites sepiaria*— percent weight loss and resistance class				Decay by *Lenzites trabea*— percent weight loss and resistance class			
		0–10— very resistant	11–24— resistant	25–44— moderately resistant	45+— non-resistant	0–10— very resistant	11–24— resistant	25–44— moderately resistant	45+— non-resistant	0–10— very resistant	11–24— resistant	25–44— moderately resistant	45+— non-resistant
		Percent of Samples											
Longleaf pine	29	0	10	62	28	38	31	24	7	48	21	24	7
Eastern white pine	25	8	4	24	64	32	20	32	16	44	16	4	36
Sugar pine	34	0	0	47	53	3	12	59	26	3	12	29	56
Loblolly pine	29	4	0	10	86	24	17	35	24	34	14	21	31
Ponderosa pine	35	3	0	6	91	23	31	23	23	51	23	9	17
Jack pine	20	0	0	0	100	0	5	60	35	5	20	45	30
Western hemlock	14	0	0	0	100	0	0	7	93	0	0	0	100
Lodgepole pine	28	0	0	4	96	0	0	0	100	0	0	0	100
Red pine	35	0	0	0	100	9	9	45	37	17	20	43	20
White fir	32	0	0	0	100	0	0	0	100	0	0	0	100
True fir[2]	25	0	0	0	100	0	0	0	100	0	0	0	100
Western white pine	20	0	0	0	100	0	0	0	100	0	0	10	90
Engelmann spruce	20	0	0	0	100	0	0	0	100	0	0	0	100

[1]Arranged in decreasing order of average resistance shown to *Poria monticola* (see Fig. 1).

[2]The results of the decay tests with 16 samples of unidentified true fir and 9 samples of noble fir are shown together since no significant difference was found between the 2 lots.

tain uses where moderate decay hazard exists.

A logical basis of comparison for this purpose is the proportion of samples in each species that showed moderate or greater decay resistance. Since the proportions are neither the same nor the species entirely in the same order in resistance to decay by the different test fungi, and since the three fungi are presumed to be of equal prominence in any general comparison, the average proportion for the three fungi is used here. These average proportions of pine samples showing moderate or greater resistance, as determined from the data given in Table 2, are as follows:

Pine species:	*Percent*
Longleaf	86
Eastern white	65
Sugar, loblolly, ponderosa	53–56
Jack, red	45–48
Lodgepole, western white	1–3

In such a listing the figure for hemlock, true fir, and spruce would be zero.

For the purpose of orientation, the evidence from these and previous tests of the same kind is that the heartwood of longleaf and possibly eastern white pine could be placed on a par for decay resistance with that of Douglas-fir (Englerth and Scheffer, 1954; Scheffer and Englerth, 1952). All of these woods can be classified as moderately resistant. The sugar, loblolly, and ponderosa pines also appeared comparable to Douglas-fir in resistance to *Lenzites trabea,* but not to *Poria monticola.* It must be emphasized here that the foregoing comparisons pertain strictly to the heartwood of the various species, and, therefore, have definite practical limitations. It is becoming increasingly difficult to get all-heartwood lumber, particularly of pine species, as the cut of second-growth timber increases. The sapwood of all species lacks decay resistance.

European investigations of the pinosylvins (phenolic compounds) in Scotch pine (Erdtman, 1955) provide a chemical explanation for variation in decay resistance of pine heartwood both within and between trees of the same species. Pinosylvins have been shown to be the chief material accounting for most of the resistance of the pines to attacks by insects and decay fungi. In 70 percent of Swedish-grown Scotch pine trees, the outer heartwood contained more pinosylvins than the inner heartwood. Further, the content of pinosylvins varied among different trees, relatively large amounts being present in only a small percentage of cases. The pinosylvin content apparently was not directly related to the growth environment or growth rate of the tree, but seemed to be determined genetically, with some evidence of variation identifiable with local races of the species. Similarly, evidence of genetic variation in decay resistance has been reported for black locust and certain oaks (Scheffer *et al.,* 1949; Scheffer and Hopp, 1949).

An attempt was made to estimate the diameter of the source trees at points where the samples were taken by measuring the curvature of the growth rings. Material associated with the larger diameters tended to be somewhat more resistant than that from the smaller diameters in some of the pines. However, since the error in estimating large diameters from the ring curvature of small samples is considerable, no specific data are presented.

Genetic improvement of the heartwood decay resistance of some pine species appears possible through selecting trees such as those represented by the samples showing comparatively high resistance. Species in this test group potentially most amenable to significant genetic improvement in resistance apparently include longleaf, eastern white, loblolly, and ponderosa pine. Within these species, trees that have wood with superior resistance to a wide variety of decay fungi might be selected for propagation. For example, all of the samples that incurred no more than 24 percent weight loss when exposed to *P. monticola* showed no more than 10 percent loss when exposed to either *L. sepiaria* or *L. trabea.*

Summary

The following woods were exposed in laboratory tests to decay by *Poria monticola*, *Lenzites sepiaria*, and *L. trabea:* eastern white pine, jack pine, loblolly pine, lodgepole pine, longleaf pine, ponderosa pine, red pine, sugar pine, western white pine, noble fir, white fir, western hemlock, and Engelmann spruce. From 9 to 35 heartwood samples of each species, each sample representing a different tree, were tested.

Moderate decay resistance to all three test fungi, comparable to that of Douglas-fir, was indicated for longleaf pine and possibly eastern white pine. Varying degrees of moderate decay resistance to two of the three test fungi were indicated for ponderosa, loblolly, sugar, jack, and red pine. The other wood species showed low decay resistance to all fungi.

The range of resistance among samples of the same woods was shown to be exceedingly wide for those species that were classed as moderately resistant. In the comparatively nonresistant woods, variation in amounts of decay tended to be relatively small. Among the more resistant species of this test, samples with decay resistance ratings of "very resistant" and "resistant" were common. This suggests the possibility of using trees with such highly resistant wood in forest tree improvement programs.

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Further Applications of Skewness and Central Tendency Tests with the Rectangular Distribution as a Criterion

BY
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CHERNG-JIANN SHIUE

TESTS OF SKEWNESS and central tendency in comparison with the rectangular distribution have been suggested by the authors (1957)[1] to classify the spatial relationships of trees and plants. The method can be applied to many fields of forest research. Three sets of field data drawn from other experiments are provided here to illustrate the use of the general method in studies of reproduction, tree breeding and thinning; in addition, a theoretical use in determining logging costs is suggested.

But before going into the particulars of these studies, consider what is meant in general by the varying combinations of skewness and central tendency. Imagine a particular forest area having a given number, size and species of arbitrarily movable trees (or analogously, a fixed number of tiny, moveable dots on this page). Now arrange the trees so that each is approximately equidistant from its immediate neighbors. Then, for the sake of clarity of exposition, select a plot size sufficiently large that its dimensions are greater than the equidistant spacing of the trees. (If the plots were smaller it would merely mean that there is some probability of obtaining a certain number of "empty" plots, even in the case of an evenly spaced forest). Assume that sufficient plots are taken so as to represent the forest and avoid the edge effect of its perimeter. The resulting classification would be positive central tendency significant, symmetry predominant, i.e., an "even" spatial distribution of trees, where the strong central tendency is represented by plots having, say, two or three trees each.

Now rearrange the trees in this hypothetical forest so that it contains a few small, circular openings, which will, by definition, increase the density of trees on the non-

[1]Shiue, Cherng-Jiann and Ronald Beazley. 1957. Classification of the Spatial Distribution of Trees Using the Area Sampling Method. For. Sci. 3:22-31.

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open area. Similarly sample it. The result would likely show a few "zero" plots, a few with one tree per plot, numerous "two's," many "three's," and quite a few "fours." The resulting frequency distribution may well classify as positive central tendency significant, negative skewness significant, since it picks up the effect of the open areas, their edge effect and the increased density on the non-open area. If the few openings involved had the same area but were long and narrow, instead of circular, the classification would tend to indicate the fewer "zero" plots and the greater number of "one's" and "two's" (brought about by the greater edge effect) by showing positive skewness predominant rather than positive skewness significant.

Again rearrange the trees in the forest, this time so that there is a greater total "open" area represented by a moderate number of large, circular open areas. This time the results of similarly sampling the forest may show negative central tendency predominant with symmetry predominant, because of a large frequency of "zero" plots, relatively fewer "one's," "two's" and "three's" but with many "four's" and "five's" (due to increased density on the "non-open" areas). Other things being equal, if only the shape of these opening were changed from circular, to say, long and narrow, fewer "zero" plots would occur and more "one's," "two's" and "three's" with still about the same, relatively large number of "four's" and "five's," probably bringing about a classification wherein negative central tendency may still be significant but skewness would be negative and predominant rather than symmetric. Continuing to use the same total "open" area (large) but arranging the open areas so that they are more numerous and smaller, the resulting classification may well become standard central tendency and symmetry predominant, i.e., a rectangular distribution, because of the "zero" plot frequencies being increased slightly, the "one's," "two's" and "three's" being increased relatively greatly (increased edge effect) and the "four's" and "five's" being reduced somewhat — all of which tends to "even out" the frequency distribution when plotted on a graph.

Finally, rearrange the trees once more so that there is relatively a very great amount of open space represented by a large number of large, circular openings. The results of sampling such a forest would indicate a very high frequency of "zero" plots, a moderate number of "one's," "two's," "three's," and "four's" due to edge sampling, and a minor number of say "five's," "six's" and "seven's" due to the high density on the small, non-open areas. Very likely the forest would now classify as negative central tendency predominant, positive skewness significant. If the openings were made long and narrow or very irregular in shape, the frequency of "zero's" may remain large but still be reduced somewhat, while the "one's," "two's," "three's," "four's" may increase to a moderate number, the "five's," "six's," and "seven's" remaining minor in frequency. In this case the classification would probably be indicated by standard central tendency, positive skewness predominant.

In similar manner, with a given hypothetical forest having a fixed area and a fixed number of trees, almost any degree of combination of skewness and central tendency may be achieved, simply by juggling the total area of "open" space, the number (and thus size) of spaces and the shapes of the open spaces, each of which provides a unique combination. The general method of classification suggested by Shiue and Beazley (1957) groups the infinite number of such combinations into 25 classes.

In addition to varying the total area of "open" spaces and their number and shape, the restriction of a fixed total number of trees may be relaxed and permitted to vary also, which would further change the combinations of skewness and central tendency obtained as well as changing the size classes

(numbers of trees per plot) which compose the frequency distribution. Finally, to approach a description of a real forest situation *in toto*, combinations of skewness and central tendency may be measured for each species and size class from a single sampling, where the group of such classifications may be said to describe the spatial relationships of the entire forest. Naturally, as the tree size classes become markedly smaller, correspondingly smaller plots should be used. If there is a wide variation in size classes of interest in a particular forest, smaller plots may be included within the larger ones.

In the examples which follow it should be pointed out that the term "clumpy" is a relative term and does not necessarily mean an association of stems which are completely surrounded by relatively open space, but rather refers to any group of more densely grouped stems bordered *in part* at least by some relatively open area. Furthermore, in the two examples which involve the continuous case (tree breeding and thinning) the question of size of class interval arises. In the previous paper it was pointed out that a minimum frequency of 5 is required in the mean and immediately adjacent classes. This limit may be approximated by trial and error in some cases fairly easily. The following formula will provide a class interval which approximates a minimum frequency of 5 in the mean class and the classes adjoining it.

$$\text{C.I.} \geqq \left(\frac{5R}{n}\right)\left(\frac{s^2}{1/3\,(\bar{x}^2+\bar{x})}\right) \text{ with}$$

a limit of 10 to 15 classes

where, C.I. = the proposed class interval
R = the range
n = total number of observations
$\bar{x}$ = the mean
s^2 = the variance = $\dfrac{\Sigma(x-\bar{x})^2}{n-1}$
$1/3\,(\bar{x}^2+\bar{x})$ = the variance of a rectangular distribution.

The suggested C.I. formula provides a useful trial beginning because the first expression, 5R/n, would insure class intervals having a frequency of 5 in each if the distribution were rectangular. The ratio of $s^2/1/3(\bar{x}^2+\bar{x})$ serves as an adjusting coefficient when the distribution is not rectangular. If the variance of the distribution in question is large then this coefficient is large, hence the product of it with 5R/n tends to provide a minimum frequency of 5 in the mean class and each of the adjacent classes.

The proposed C.I. would permit a very large number of classes to be used when n is itself very large. Since such a large number of classes tends to destroy the distribution, the number of classes should be limited to 10 to 15, to act as an upper limit on class number, which is not restricted by the C.I. formula. Normally the class interval is, of course, centered on the nearest integer.

In the tree breeding and thinning cases which follow the reproduction example, it was not possible to follow the above rule because the data were collected originally without thought of their use in these tests. However, this does not otherwise detract from their usefulness.

Reproduction Study

Number of seedlings per unit of area and the evenness of seedling distribution are two main factors which measure the effectiveness of reproduction. In the skewness and central tendency tests, negative skewness and positive central tendency together tend to indicate an even, light density distribution of seedlings on the ground, while positive skewness and negative central tendency represent clumpiness of seedlings, which are, of course relatively densely associated within clumps.

An apparently homogenous aspen stand was divided into halves, one of which was treated with sodium arsenite for the purpose of chemical debarking. Both were clear cut. Although some confounding may be present due to the imperfect statistical design involved, none the less the hypothesis

was made that treatment with sodium arsenite brings about a more desirable distribution of suckers after cutting, *for the purpose of this example only*.

Eighty milacre plots were established on each of the two aspen cutover areas. Numbers of suckers in each plot were counted. Any plots occupied by three or more suckers were tallied in the three-sucker class since the investigator considered three or more suckers in each plot as the ideal requirement for effective reproduction. Plots with successively fewer suckers than three are considered linearly less desirable. The results are given in Table 1.

The conclusion is that the suckers on the check area tend to be clumpy, showing a moderate number of "open" spaces and a moderate number of partially open spaces with a relatively smaller well-stocked area. The debarking area, on the other hand, shows relatively less clumpiness, fewer open and partially open areas and relatively more well-stocked area. Ideally the tests would show positive central tendency significant, symmetry predominant, indicating a distribution of trees on the ground which are all evenly spaced. At its worst the frequency distribution would show negative central tendency significant, positive skewness significant, indicating an extreme

TABLE 1. Skewness and central tendency tests on aspen reproduction.

Number of suckers per plot[1]		Untreated area	Debarking area (sodium arsenite)
		Number of plots	
0		28	17
1		15	19
2		6	15
3		31	29
Total number of plots		80	80
Average number of suckers per plot		1.5	1.7
Skewness Test	Departure	0.038[2]	−0.012
	Probability	>0.25	>0.25
	Type of distribution	Symmetry predominant	Symmetry predominant
Central Tendency Test	Departure	−0.1187[3]	−0.0248
	Probability	<0.05	>0.25
	Type of distribution	Negative central tendency significant	Standard central tendency predominant
Interpretation of the distribution in spatial relationships of suckers.		Clumpy, numerous open spaces, suckers unevenly spaced.	Slightly clumpy, fewer open spaces, suckers relatively even spaced.
Desirability		Undesirable	Relatively more desirable

[1]Discrete case.

$$^{2}d_{s} = \frac{28 + 15}{80} - 0.500 = 0.538 - 0.500 = 0.038$$

$$^{3}d_{c} = \frac{0.5 \times 15 + 0.5 \times 6}{80} - \frac{1}{1.5 \times 2 + 1} = 0.1313 - 0.2500 = -0.1187$$

amount of large open spaces with suckers jammed together on the few occupied areas.

Tree Breeding Study

To select varieties, lines or hybrids having more desirable characteristics is the main part of tree breeding work. In evaluating the desirable characteristics, the mean value and its variance for each variety, line or hybrid serve as the standards for selection. Varieties, lines or hybrids with more desirable mean and smaller variance have been the goals to be sought. When any measurements of individuals within the same variety, line or hybrid are classified into a frequency distribution, the tests of skewness and central tendency of such a distribution will give much more information than does the variance alone. For instance, two hybrids of aspen provide the same mean growth and variance but different frequency distributions; one shows a positive central tendency and the other indicates negative central tendency. Consequently the former hybrid has more uniform growth since more individuals are represented near the mean class than the latter, hence the former is more desirable.

In the Cloquet Experimental Forest, an extensive jack pine seed source study has been carried out. In comparing hardiness to winter injury, trees from each seed source were classified into five groups according to the percent of crown killed. Frequency distributions by winterkill class of trees from Wellston, Michigan and Baldwin, Michigan show striking differences (Table 2).

In this seed source test there is no question of areal or spatial distribution involved (although such a spatial distribution could have been measured if desired, by using areal plots). Instead, it measures the distribution of degree of winter injury by injury classes. In the particular case illustrated in Table 2 the typical measures of goodness, i.e., the mean and variance, would have indicated fairly well that the Wellston seeds are better than those from Baldwin, but not as clearly as the skewness and central tendency tests do. It may very well have happened that the mean of both the Wellston and Baldwin tests turned out to be the same, say 1.47, and furthermore, that their variances were equal. On this basis alone, one could conclude only that they were equally good relative to winter injury. Actually, the Wellston seeds could have been much better if their distribution showed positive skewness significant while the Baldwin seeds indicated negative skewness significant. This is so because the Wellston seeds would then be represented by a greater proportion in the "0" and "1" classes and a smaller proportion in the "2," "3," and "4" classes than the Baldwin seeds.

Thinning Study

The purposes of thinning are to increase the forest growth, both in quantity and quality, to improve stand composition, to promote sanitation and to obtain greater total yield. An adequate thinning will make enough room for the growth of individual trees within the stand; and competition among trees should be minimized to avoid loss by mortality. When a stand is tallied in a stand table form, showing the frequency distribution of trees by diameter classes, the tests of skewness and central tendency will provide information as to the degree of competition within the stand. In an even-aged stand, positive skewness and negative central tendency indicate a great number of trees in the small size classes, and show the presence of severe competition, while negative skewness and positive central tendency indicate a fast-growing, healthy forest. Data from some even-aged red pine thinning plots in the Cloquet Experimental Forest are used here to illustrate these tests (Table 3).

In this thinning study, because the check plot has severe competition, as indicated by the presence of some large trees and many very small ones, it can be said that the 7′ x 7′ spacing is a healthy stand with

sufficient room for growth. But positive central tendency with symmetry in itself indicates only uniform growth, which could be brought about by uniform stagnation of the stand. In such a case the growth would have been uniformly very slow for the age class concerned and thus seriously competitive. On the other hand, positive central tendency and a large average diameter compared to a known, fast rate of diameter growth indicates a healthy stand without serious competition.

Possible Use in Estimating Logging Costs

Two of the major physical factors affecting the cost of thinning and logging are the topography and the spatial distribution of species to be cut. Usually the effects of topographical differences on costs are estimated subjectively on the basis of the appraiser's past experience, as is the tree distribution factor. Although the skewness and central tendency tests may not as readily indicate the effect of topography on

TABLE 2. Skewness and central tendency tests on winterkill of trees from two sources.

Winter injury class[1]		Seeds from Wellston	Seeds from Baldwin
		Number of trees	
0 (no killing)		50	1
1 (1 to 33% killed)		44	5
2 (34 to 66% killed)		63	6
3 (67 to 99% killed)		25	29
4 (dead)		9	4
Total number of trees examined		191	45
Average class of winter injury		1.47	2.67
Skewness test	Departure	−0.015[2]	−0.124
	Probability	>0.25	<0.05
	Type of distribution	Symmetry predominant	Negative skewness significant
Central tendency test	Departure	0.0233[3]	0.3181
	Probability	0.05<P<0.25	<0.05
	Type of distribution	Positive central tendency predominant	Positive central tendency significant
Interpretation of the distribution		Most trees have moderate winter injury as the mean value; the number of trees distributed on both sides of the mean is approximately the same.	Great number of trees with the winter injury heavier than the mean value. Most of the trees are distributed above the mean class.
Desirability		Relatively more desirable	Undesirable

[1]Discrete case; uneven sample sizes.

$$^{2}d_s = \frac{50 + .97\,(44)}{191} - 0.500 = 0.485 - 0.500 = -0.015$$

$$^{3}d_c = \frac{0.53 \times 44 + 0.47 \times 63}{191} - \frac{1}{1.47 \times 2 + 1} = 0.2771 - 0.2538 = 0.0233$$

TABLE 3. Skewness and central tendency tests of stand tables from a homogenous forest after different intensities of thinning, 25 years later.

	Diameter class (inches)[1]	Check plot	4' x 4' spacing plot	7' x 7' spacing plot
			Number of trees	
	1 (0.5—1.4)	7		
	2 (1.5—2.4)	26	24	1
	3 (2.5—3.4)	35	70	4
	4 (3.5—4.4)	24	49	10
	5 (4.5—5.4)	10	45	13
	6 (5.5—6.4)	5	23	21
	7 (6.5—7.4)	1	3	21
	8 (7.5—8.4)			10
	9 (8.5—9.4)			2
	Total number of trees	108	214	82
	Average diameter	3.21"	3.92"	5.98"
Skewness test	Departure	0.356[2]	0.0354	− 0.0356
	Probability	$0.05 < P < 0.25$	$0.05 < P < 0.25$	> 0.25
	Type of distribution	Positive skewness predominant.	Positive skewness predominant.	Symmetry predominant, very close to $P = 0.25$.
Central tendency test	Departure	0.1182[3]	0.0302	0.1425[4]
	Probability	< 0.05	$0.05 < P < 0.25$	< 0.05
	Type of distribution	Positive central tendency significant.	Positive central tendency predominant.	Positive central tendency significant.
	Interpretation of the distribution	Severe competition exists; great number of trees in the small size classes.	Severe competition still exists; great number of trees in the small size classes.	Most trees have enough room for growth, great number of trees in the large size classes.
	Condition of stand	Unhealthy, slow growing and high mortality.	Unhealthy, slow growing and high mortality.	Healthy, fast growing and very low mortality.

[1]Plot sizes are not the same (number of trees is not relevant). Continuous case.

$$[2]d_s = \frac{7 + 26 + 35\,(3.21 - 2.5)}{108} - 0.500 = 0.5356 - 0.5000 = 0.0356$$

$$[3]d_c = \frac{0.21 \times 24 + 0.79 \times 35}{108} - \frac{1}{2(3.21 - 0.5)} = 0.3027 - 0.1845 = 0.1182$$

$$[4]d_c = \frac{0.02 \times 13 + 0.98 \times 21}{82} - \frac{1}{2(5.98 - 1.5)} = 0.2572 - 0.1116 = 0.1425$$

costs, they could be used to measure the effect of tree distribution. Granting that in many cases topographical slope may have the greatest net effect on cutting and logging costs, the possibility of initially classifying the distribution of trees concerned into one of the groups permitted by the tests would at least allow the distribution factor to be consistently measured and associated with the costs experienced. It is possible also

to measure the percentage of swamp which occurs on each plot and to assess this topographical factor. Then the combinations of given classifications of the distributions of trees and swamps could be associated with logging costs, by total size and method of operation within regions. Thus a single sampling of this nature could provide the data necessary for typical timber volume estimates as well as a further assessment of partial (tree and swamp distribution) logging costs by individual species or groups of similar species, and simultaneously, a functional description of reproduction and young growth, where appropriately smaller plots are included within some or all of the larger ones. At present there are no records of costs in conjunction with pre-cut sampling of the type described available to the authors, hence an applied case cannot be presented. However, it is hoped that such results may become available in the future.

Forest Nursery Practice in the Lake States

By J. H. Stoeckeler and G. W. Jones. U. S. Dept. Agric. Agricultural Handbook No. 110. 1957. 124 pp. Washington, D. C. $2.00.

Review by C. F. Korstian
School of Forestry, Duke University

This handbook is another outstanding contribution which will be most welcome to the forestry profession, especially in the Lake and Northeastern States and adjacent Canada. It is a long overdue companion to the publication on "Forest Plantations in the Lake States"[1] which has taken its appropriate place in our technical literature.

A careful reader of the handbook can readily discern that many of the practices have developed, not as a result of trial and experience alone, but also from underlying research and keen observations of many individuals during the past quarter century, all of which contribute toward the value of the handbook.

The authors are to be complimented on the thoroughness with which they have treated the different operations from the collection, extraction and storage of seed, through the selection and development of nursery sites, equipment and personnel, to the various nursery practices and protection against unfavorable weather, mammals, birds, insects and diseases.

This publication is no exception to those that emphasize the mechanization of forest nursery operations in the United States. Yet it is somewhat surprising to see a number of manually or horse-drawn implements illustrated in the handbook which tend to give the impression that these operations are not yet as fully mechanized as is really the case.

To readers unacquainted with what may appear to be long delays in processing government manuscripts, the citing of nursery statistics in the introduction that are five years old may seem undesirble. However, many readers will understand the circumstances and know that, with the greater emphasis now being placed on forest planning, nursery production in the Lake States has probably increased as it has in other forest regions.

This handbook should be in every forestry library in the United States and Canada. Further it should be in the hands of every forest nurseryman and readily available to foresters and others engaged in forest planting in localities to which either the specific information or the basic principles may apply.

[1]Rudolf, Paul O. U. S. Dept. Agric. Tech. Bull. 1010. 171 pp. 1950.

Control of Soil Moisture Depletion Through Use of 2,4-D on a Mustard Nurse Crop During Douglas-Fir Seedling Establishment

BY
CYRUS M. McKELL
J. M. FINNIS

DIRECT SEEDING of Douglas-fir (*Pseudotsuga menziesii* Mirb. Franco) on extreme southern exposures in the Pacific Northwest may often be unsuccessful because of failure of seedlings to survive. High soil-surface temperatures and drought are responsible for a large percentage of seedling mortality. Isaac (1938) in a study of Douglas-fir establishment reported that temperatures of over 144° Fahrenheit on blackened soil surface killed all seedlings. More recently, Silen (1956) used "Tempil" pellets in studying seedling mortality. He found that melting of the 138° F. tempil indicated a lethal temperature and that by July 1 this point was reached on nearly 69 percent of the area of south slopes.

Use of an India mustard (*Brassica juncea*) nurse crop to reduce soil surface temperatures as an aid in seedling establishment has been studied the past four years as a result of its beneficial use for erosion control following an extensive forest fire in southwestern Oregon in 1951. Successful establishment of mustard for the purpose of reducing erosion on burned watersheds in southern California encouraged the U. S. Bureau of Land Management to seed India mustard and Douglas-fir by helicopter over 16,800 acres at Vincent Creek, Oregon, following a burn in the early fall of 1951. This was the first time that mustard had been used for rehabilitation of Douglas-fir lands in the Northwest. In the spring following seeding, inspection indicated good erosion control. The best stands of mustard were obtained at an elevation of 700 feet on southern exposures. Mustard growth was less at higher elevations and on northern exposures. Although no unfavorable effect on Douglas-fir seed germination and seedling establishment was noted as a result of the mustard nurse crop, further study of the relationship between mustard and Douglas-fir stand establishment appeared necessary before recommendations could be made. Therefore, a cooperative research project was developed between the Bureau of Land Management and Oregon State College.

Initial studies were made on field plots by Pierovich[1] on two burned areas, one

[1]Pierovich, John M. (1954). The use of mustard (*Brassica juncea*) as a nurse crop in direct seeding of Douglas-fir: I. Progress report to Bureau of Land Management. (Mimeographed, 33 pp.)

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near Jasper, Oregon, and the other near Viola, Oregon. From results on these plots Pierovich and Hunt (1955) reported that soil surface temperatures were lower and that greater seed germination could be obtained under a nurse crop than in the open. However, the mustard nurse crop appeared to compete strongly for soil moisture. Pierovich suggested that problems of moisture supply could be overcome by fall sowing or by the use of herbicides as a possible means of hastening mustard maturity to reduce competition for moisture.

Clarkson[2] the following year found that sowing mustard in the fall did not eliminate the drought problem. The mustard plants remained in a rosette stage during the winter and with the advent of spring resumed growth but failed to mature sufficiently in advance of the period of high moisture stress for Douglas-fir seedlings. As a result most of the Douglas-fir seedlings died late in the spring from drought even though they had been previously protected from high soil surface temperatures by the presence of the nurse crop.

Further study of the management of a mustard nurse crop was carried on during 1955-56 by McKell.[3] Results of this study are presented here. Consideration was given to the use of 2,4-D to control the deleterious moisture removal by the nurse crop without interfering with its beneficial moderating effect on soil surface temperature.

Experimental Procedure

The experimental area, a clear-cut tract of approximately 40 acres on Aiken clay loam soil, at 1500 ft. elevation, was chosen in the coast range 20 miles west of Roseburg, Oregon. The slash was burned in September, 1955, the burn being clean and of moderate intensity. The area is characterized by a moderate summer drought and annual rainfall averages 30 inches, generally occurring in the fall, winter, and spring.

Experimental plots were located on a 20-25 percent slope with a general south exposure. Three 200′ x 25′ study plots were laid out on uniform sites and adjacent to each a control plot 200′ x 15′ was established. Study plots were broadcast seeded by hand on October 17 with India mustard at a rate of 35 pounds per acre. On the same day Douglas-fir seeds coated with endrin methocel rhoplex, a rodenticide similar in action to tetramine as reported by Finnis (1955), were sown with a "cyclone" hand seeder at a rate of one pound per acre over the entire 40-acre clearing to provide a buffer zone for the experimental plots. Seeding was done at a rate one-half pound higher on the study plots and control plots.

Ten circular milacre sampling areas were located in each mustard study plot and in each of the control plots. Plaster-of-paris electrical resistance blocks with a resistance reading of 450 $\pm$ 50 ohms in distilled water were made by the authors according to the method described by Bouyoucos and Mick (1940). These blocks were buried at depths of 4 and 12 inches on 6 of the 10 milacre sampling areas in each seeded and control plot. Maximum thermometers were placed in the surface one-eighth inch of soil on plots equipped with soil moisture measuring apparatus.

Moisture and temperature readings were started on May 14 and were repeated every two weeks during the spring and summer. Newly emerged Douglas-fir seedlings were identified every two weeks by placing a dated pot label in the ground beside each new seedling.

On May 5 one-half of each 200′ x 25′

[2]Clarkson, Quentin D. (1955). The use of mustard as a nurse crop in direct seeding of Douglas-fir: II. Progress report to Bureau of Land Management. (Mimeographed, 11 pp.)

[3]McKell, Cyrus M. (1956). Use of a nurse crop in Douglas-fir seedling establishment: III. Progress report to Bureau of Land Management. (Mimeographed, 30 pp.)

mustard seeded plot and half of the adjacent control plot were sprayed with butyl ester 2,4-D at a rate of three-quarter pounds in 40 gallons of water per acre. Mustard plants were between 18 and 30 inches in height and were in blossom at this time, but no seed pods had started to form.

Results and Discussion

Seedling emergence was greater on mustard plots where 301 seedlings were tallied than on the control plots, where the seedling count was 110. The problem was, and is, to maintain this initial superiority by protecting the Douglas-fir seedlings from high temperature and drought.

Moisture appeared to be readily available at 4- and 12-inch depths on all sampling areas during April and the first three weeks of May (Fig. 1). During this period most of the Douglas-fir seeds germinated and started growth. Lack of moisture could not be cited as a primary cause of mortality except in cases where seedling roots did not penetrate the soil fast enough to escape dessication in the dry soil surface.

Soil surface temperatures on the nurse crop plots averaged 20° F. lower than on control plots on May 19 when seedling emergence was maximum. By June 16 this average temperature differential gradually decreased to zero except on mustard plots that were sprayed with 2,4-D (Fig. 2). Precipitation of 0.36 inches was recorded at a nearby weather station (Table 1) two days before spraying with 2,4-D on May 5. Additional precipitation of 1.06 inches on May 6 and 7 had the effect of minimizing the greater depletion of soil moisture by the dense mustard nurse crop up to this time and served to equalize the moisture content under the nurse crop and in the open. Except for .23 inches on June 13 no further significant precipitation was recorded until September 25.

Resistance readings, three and one-half weeks after spraying with 2,4-D show the effectiveness of the herbicide in reducing soil moisture that would have been used by the nurse crop (Fig. 3). The final reading of the Bouyoucos blocks on July 25 shows a continuing favorable moisture condition for seedling survival on sprayed plots at the 12-inch depth. In addition, the 2,4-D application on the control plots reduced the rate of soil moisture depletion by native shrubs and weeds following the slash burn. Thus a suitable herbicide application might prove feasible when native vegetation may compete too strongly for moisture to allow successful Douglas-fir seedling establishment.

The results indicate that both favorable temperature and moisture conditions can be maintained if a nurse crop is planted and later sprayed with a selective herbicide. An earlier date of spraying could be used to control growth of the nurse crop and to prevent early losses of soil moisture if Douglas-fir seedling emergence is sufficiently completed. Although soil moisture reserves were high for plots not planted to a nurse crop, these plots did not receive the benefit of the lower soil-surface temperatures associated with the nurse crop. Soil-

TABLE 1. Precipitation at Reston, Oregon during the 1956 growing season.

Day	Precipitation each two-day period				
			Inches		
1-2	.05	.03	.12		
3-4		.36	.05		
5-6	.17	.46			
7-8	.01	.66			
9-10	.22	.06		.02	
11-12	T	.01			
13-14			.26		
15-16			.01		
17-18			.36		
19-20					
21-22					
23-24					
25-26	.01	T			
27-28					
29-30					
31					
Total	.46	1.65	.80	.02	.00
	April	May	June	July	Aug.

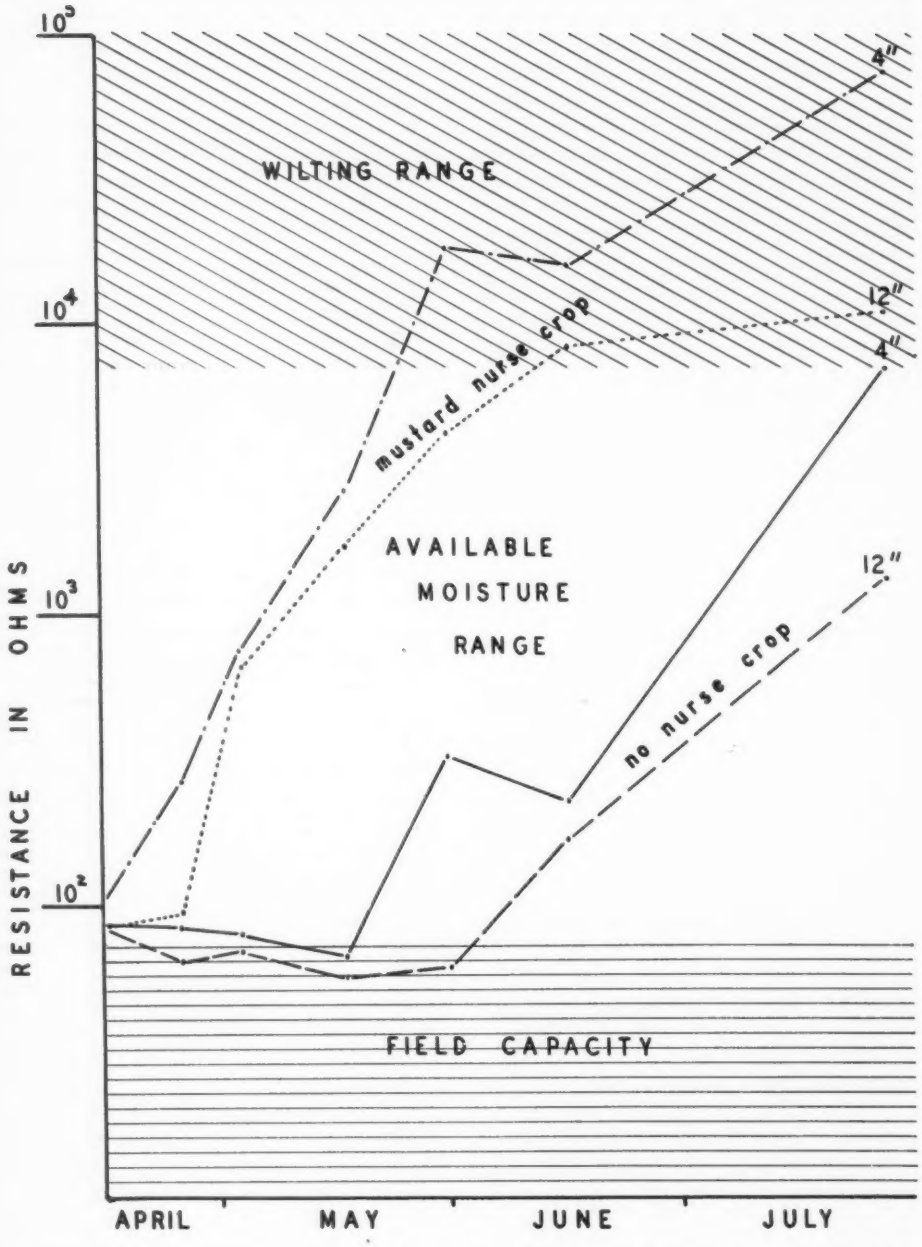

FIGURE 1. *Mean resistance readings in ohms at 4- and 12-inch soil depths on nurse crop and no nurse crop plots from May 14 to July 25, 1956. Readings are from plots not sprayed with 2,4-D.*

surface temperatures on the nurse crop plot averaged 12° F. lower than plots with no nurse crop during April and May, the two months of seedling emergence.

Douglas-fir seedlings did not exhibit an immediate sensitivity to the low rate of 2,4-D application, but it was difficult to distinguish between damage to Douglas-fir seedlings from 2,4-D and that from other causes. However, 2,4-D had an adverse effect on seedling survival, whether under mustard or in the open (Table 2). A Chi-square test indicates a significant difference at the one percent level between seedling survival on sprayed and on unsprayed plots.

Mustard plants were extremely sensitive to 2,4-D. Stems became twisted in a few days and growth stopped within two weeks. Partly developed inflorescences ceased to grow and no seeds were produced. Foliage and stems lost most of their green color but the leaves remained attached to the stems; an important feature that would provide shade even if the nurse crop were sprayed earlier in its development.

Further work is needed to find a spray technique or herbicide that is effective in killing the mustard but not toxic to the Douglas-fir seedlings. This would result in maintaining the benefit of the increased germinatiton and lower soil-surface temperature condition under the mustard nurse crop cover.

TABLE 2. Douglas-fir seedlings surviving six weeks following application of 2-4,D.

Treatment	Number Surviving May 5	Number Surviving June 16	Percent Survival
	Under Mustard		
Sprayed	119	63	52.9**
Unsprayed	106	94	88.6
	No Mustard		
Sprayed	51	24	47.0**
Unsprayed	28	21	75.0

**Significant at the .01 level.

Summary

A mustard nurse crop can be used to reduce high soil-surface temperatures in Douglas-fir seedling establishment. This practice has met with the accompanying problem of excessive soil moisture depletion by the nurse crop and decreased Douglas-fir seedling survival. Prevention of rapid moisture depletion during spring months is very important in preventing seedling losses where the period of summer drought may be from 2 to 4 months.

Spraying the nurse crop with 2,4-D at a rate of three-fourths pound per acre during the full bloom stage stopped further development of the mustard but also killed some of the Douglas-fir seedlings.

Rapid depletion of soil moisture was controlled by the application of the herbicide to the mustard nurse crop. Earlier application of a spray appears to be permissible since the herbicide caused the retention of leaves by the nurse crop for a short while, thus maintaining a favorable temperature

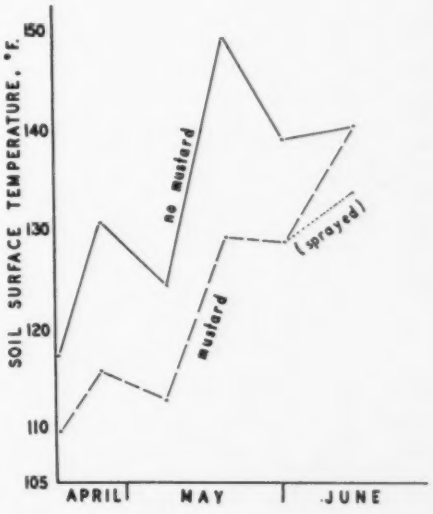

FIGURE 2. *Soil surface temperatures on Douglas-fir seedling establishment plots with a mustard nurse crop and without a nurse crop.*

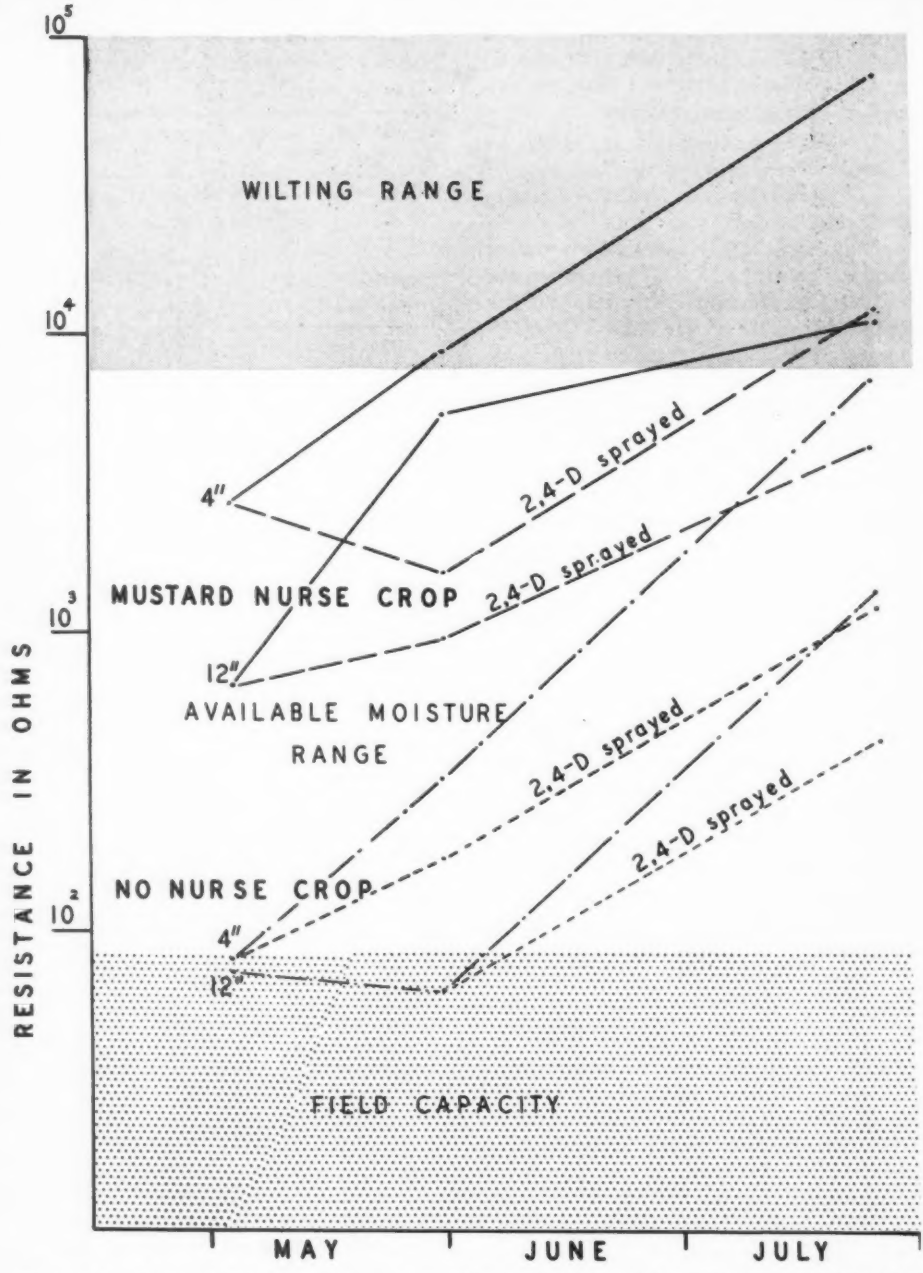

FIGURE 3. *Effect of 2,4-D spray to reduce soil moisture depletion by vegetation as indicated by mean resistance readings in ohms at 4- and 12-inch soil depths on Douglas-fir seedling establishment plots with and without a mustard nurse crop.*

condition for the Douglas-fir seedlings by continuing to provide shade.

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Protection Against Wood Deterioration

Annual Report on Wood Protection. 1955. Edited by Günther Becker and Gerda Theden. Berlin-Dahlem, Unter den Eichen 87, Western Germany.

Review by R. M. Lindgren
U. S. Forest Products Laboratory, Madison, Wisconsin

This 170 page digest of world literature on the protection of wood against deterioration was founded by Willy Kinberg about 20 years ago, and has been continued by the present editors since 1951. As in previous issues, the literature abstracted in the 1955 Edition, released in November, 1956, is confined to publications that present new data of value in developing and applying protective measures. Most of these publications appeared in 1955 or early 1956; the remainder represent previously overlooked papers from the 1952-1954 period. Beginning with this edition, the report is expected to be released annually again.

In general content, the new edition comprises about 300 pages divided into 4 sections —classification of subject matter, abstracts arranged according to this classification, bibliography, and index. The abstracts are presented under the following headings: Fundamentals of Wood Protection; Wood-Destroying Organisms and Their Influence; Wood Protection Against Organisms; Fire-Retarding Wood Protection; Wood Protection Against Chemical Agents; Economic Aspects and Statistics; Reports on Scientific Institutes; Associations, Conventions, International Cooperation; and Personal Notes.

The abstracts, which range from 20 to 200 or more words, are given in both German and English, on facing pages. They carry the author's name and are numbered consecutively, which makes it easy to trace each abstract to its literature source in the bibliography. A new feature is the inclusion of marginal notes to facilitate the search for abstracts of special interest within the broad subject groupings. Also, literature on marine organisms in wood is covered intensively for the first time. With few exceptions, the survey made of literature seems adequate, quality of abstracts is high, and the arrangement of literature under the subject-matter headings seems logical.

The task undertaken by the editors is a large one that has its only reward in the service it performs. Such service undoubtedly will be great if copies of this and subsequent reports are obtained by, or made accessible to, all research workers engaged in wood protection problems. The editors certainly warrant at least this evidence of encouragement and gratitude.

Association of Yeasts with the Douglas-Fir Beetle

BY
K. C. LU
DONALD G. ALLEN
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THE DOUGLAS-FIR BEETLE (*Dendroctonus pseudotsugae* Hopkins) is economically important in relation to Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) in the western United States. There is reason to believe that this insect might be controlled most economically by certain indirect methods. The relation of some wild yeasts to other *Dendroctonus* species is generally known, and suggests one approach toward a solution of the problem.

Various aspects of the relationship between insects and microorganisms have been described by Steinhaus (1946), Pant (1950), and Shihata (1952). Beck (1922) isolated a new species of yeast (*Endomyces bisporus*) from the galleries of *Ips typographus* (L.) attacking spruce in Austria. Wickerham (1951) renamed it as *Hansenula beckii* (Beck) because it utilizes nitrate ions, a typical characteristic of the genus. The first mention of the association of yeasts with blue-staining fungi and bark beetles appears to be that of Grossman (1930). Three non-fermenting types of yeasts were described. Person (1931) reported the occurrence of a yeast in beetle-attacked trees and stated that the aroma of yeast fermentation in the tree probably attracted more beetles from greater distances. No description of the yeast was given. Rumbold (1931) reported the presence of yeasts and bacteria in association with bark beetles and blue-staining fungi. Leach *et al.* (1934) called attention to the presence of yeast in the interrelation of bark beetles and bluestain but gave no details as to the types of yeasts. Holst (1936) found a new yeast, *Zygosaccharomyces pini*, n. sp. generally associated with *Dendroctonus* and *Ips*. He concluded that *Saccharomyces pini* is the most common yeast found in *D. brevicomis* Lec. and *Candida silvicola* is most prevalent in *Ips oregoni* (Eichh.).

The purpose of the present cooperative study is to help prepare the way for determining what can or cannot be done with yeasts in combatting the Douglas fir beetle.

Two distinct phases of the study are: The identification of yeasts isolated from specimens of the insect selected at random in its natural environment, and from galleries of current infestations in freshly collected inner bark; and tests to determine

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what, if any, fermentation products involved are attractive to the beetle.

General Nature and Sources of Sample Material

Beetles and currently infested bark were collected for culture purposes. Large numbers of beetles, in addition, were collected for tests of attractants. Special care was taken to avoid field contamination of samples intended for culturing. Beetles were collected with sterilized forceps, and bark was wrapped in new cellophane as it was removed from the tree or log. All samples not used upon reaching the laboratory were stored in a cold chamber at about 40°F. Beetles collected in warm weather, especially far from the laboratory, were distributed in small numbers in each of a number of sterile bottles which were placed in crushed ice in a camp cooler carried in the car for the purpose.

All samples were obtained from inhabited galleries (except uninfested checks) and from natural wild areas. Specimens were collected from February, 1953, through the summer of 1955, as circumstances permitted. Three main collection areas were used, all in western Oregon. Most of the samples were gathered at Marys Peak, Benton County, in the Coast Range Mountains; some were gotten from the Long-Bell area in western Lane County, west of Eugene (also in the Coast Range Mountains), and a few were gathered in the Willamette National Forest, in eastern Lane County, on the west slope of the Cascade Mountains.

Isolation and Identification of Yeasts

For gross flora, beetles were dipped in a 0.5 percent solution of $HgCl_2$ for 3 minutes, rinsed twice with sterille distilled water, crushed in a petri dish and plated. For the study of yeasts in the alimentary tracts, beetles were imbedded in sterile paraffin and dissected by the technique of Miller and Mrak (1953). The removed guts were planted in poured plates and incubated at 28°C. until colonies developed. Malt extract-yeast extract agar, Wickerham (1951), was used as the plating medium.

Yeast colonies that developed on the plates were examined and observed macroscopically and microscopically. Pure cultures were obtained by conventional plating methods. In almost all cases only one type of yeast occurred on a plate.

Twenty yeast isolates were obtained from 78 beetles. Thirteen isolates were from adult beetles, 3 from larvae and 4 from the alimentary tracts of dissected beetles. Colonies selected under the microscope were purified by plating. Each isolate was systematically studied according to the procedures of Wickerham (1951), and of Lodder and Van Rij (1952). The assimilation of carbon compounds was studied by the replica plating procedure of Shifrine, *et al.* (1954).

Of 20 isolates, 6 were sporulating and 14 non-sporulating forms. The sporulating yeasts fell into the genera *Saccharomyces* and *Hansenula.*

Saccharomyces. Two isolates were found to be quite similar to *Zygosaccharomyces pini* as reported by Holst (1936). Lodder and Kreger-Van Rij (1952) placed this species in synonomy with *Zygosaccharomyces pastoria* Guilliermond. Our isolates were almost identical with *Saccharomyces pastoria.* Lodder's system of including forms bearing hat-shaped spores with poorly fermentative species in *Saccharomyces* seems to be a radical arrangement. Shifrine, *et al.* (1956) also questioned this arrangement. The two isolates do not form a pellicle on malt extract broth and do not produce a pseudomycelium; hence, they do not fall in the genus *Pichia.*

Hansenula. Four isolates were found to be similar to *Hansenula capsulata,* with the characteristics described by Wickerham (1951).

Candida. Of these, 13 were very similar to *Candida parapsilosis,* and were like *C. mycoderma,* according to the descriptions of Lodder and Van Rij (1952). *C. para-*

psilosis is a pseudomycelium forming yeast which assimilates glucose, galactose, sucrose and maltose. Splitting of arbutin is negative. It ferments glucose, galactose weakly, sucrose weakly or not at all. No pellicle is formed in malt extract broth. The culture of *C. mycoderma* fits the description of the species as given by Lodder, *et al.* (1952); it has a very primitive pseudomycelium and rapidly forms a complete dull pellicle.

Species of *Hansenula* and *Candida* accounted for most of the isolates and appear to be generally associated with the beetles. Tables 1 and 2 show the source of isolates and the species of yeasts found in different stages of the insect.

The Attractants Study

Equipment and Methods. Tests were made for possible attractant properties of the yeast ferments. Cultures of combined yeast species and of single species were prepared and incubated usually 3 days in 100 ml. of dextrose-malt extract broth contained in 500 ml. Erlenmeyer flasks. A test culture and a control were attached each to an arm of an olfactometer. Mild aspiration was provided. In most of the runs the apparatus was darkened. In a few, daylight was admitted, and in others a small flashlight bulb provided light at the flask-ends of the runways from the central chamber of the olfactometer.

For the majority of tests a glass Y-tube modified for the purpose served as the olfactometer. In other tests an olfactometer was designed in the shape of a shallow drum with two opposite arms, tubular in shape, but with a flat, roughened, basal section for better traction. At the distal ends of these arms provision was made for light of approximately equal intensity. At the distal ends of each of the two tubes also was an attachment for the Erlenmeyer flask (Fig. 1). The whole device was provided with an elevated wooden case to support and darken it from all light sources but the intended ones (Fig. 2).

From 25 to approximately 125 selected beetles were used in each test. Time allotted for the completion of each run varied, but, after about two hours, additional time allowed seemed not to alter the result. At the end of each run, distribution of the insects was recorded. All records were statistically analyzed.

Results of Attractants Study. All cultures (Nos. 1, 2, 3) containing the 4 yeast species combined were very significantly attractive to the beetles (Table 3). The tests of pure *Candida parapsilosis* (C_1) showed the results of 3 runs to be insignificant (Nos. 4,

TABLE 1. Source of yeast isolates from Douglas-fir bark beetles.

Source	Numbers examined	Numbers showing no yeasts	Numbers of isolates studied
Adult beetles	56	9	13
Larvae	14	6	3
Alimentary tracts of adult beetles	8	0	4
Total	78	15	20

TABLE 2. Number of isolates and species of yeast from bark beetles.

Species	From adult beetle	From larvae	From alimentary tracts of adult beetle	Total No.
Saccharomyces pastoria	2	0	0	2
Hansenula capsulata	3	0	1	4
Candida parapsilosis	8	2	3	13
Candida mycoderma	0	1	0	1

TABLE 3. Attractant tests with adult bark beetles.

Test No.[1]	Culture[2]	Numbers of Beetles: Used	To culture	To control flask	Dead	Remaining in Y-tube or other olfactometer	X^2 value[3]
1	$C_1 + C_2 + S + H$	25	19	4	2	0	9.78**
2	$C_1 + C_2 + S + H$	25	19	3	3	0	11.64**
3	$C_1 + C_2 + S + H$	30	23	6	1	0	9.97**
4	C_1	103	52	40	8	0	1.57 (n.s.)
5	C_1	127	48	73	6	0	5.17* R
6	S	103	41	27	0	35	2.88 (n.s.)
7	S	106	53	18	7	34	17.28**
8	S	105	67	33	0	6	11.56**
9	H	50	14	9	0	26[4]	1.09 (n.s.)
10	H	51	14	12	0	25[4]	1.15 (n.s.)
11	H	50	15	9	0	25[4]	1.50 (n.s.)
12	C_1	50	8	14	0	28[4]	1.64 (n.s.)
13	C_1	50	8	13	0	29	1.19 (n.s.)
14	Galleried bark	103	50	11	0	41	24.93**
15	C_2	106	19	79	8	0	36.73** R
16	C_2	113	21	75	0	17	30.38** R
17	C_2	100	11	41	0	48	17.31** R
18	Fresh bark	25	2	1	0	22	0.33 (n.s.)

[1] Test Nos. 9, 10, 11, 12, 13 and 18 were 1955 collections. All others were 1953 collections.
[2] C_1 = *Candida parapsilosis*; C_2 = *Candida mycoderma*; S = *Saccharomyces pastoria*; H = *Hansenula capsulata*.
[3] * Significant; ** Very significant; (n.s.) = Not significant; R = Culture rejected.
[4] Test made with drum type olfactometer.

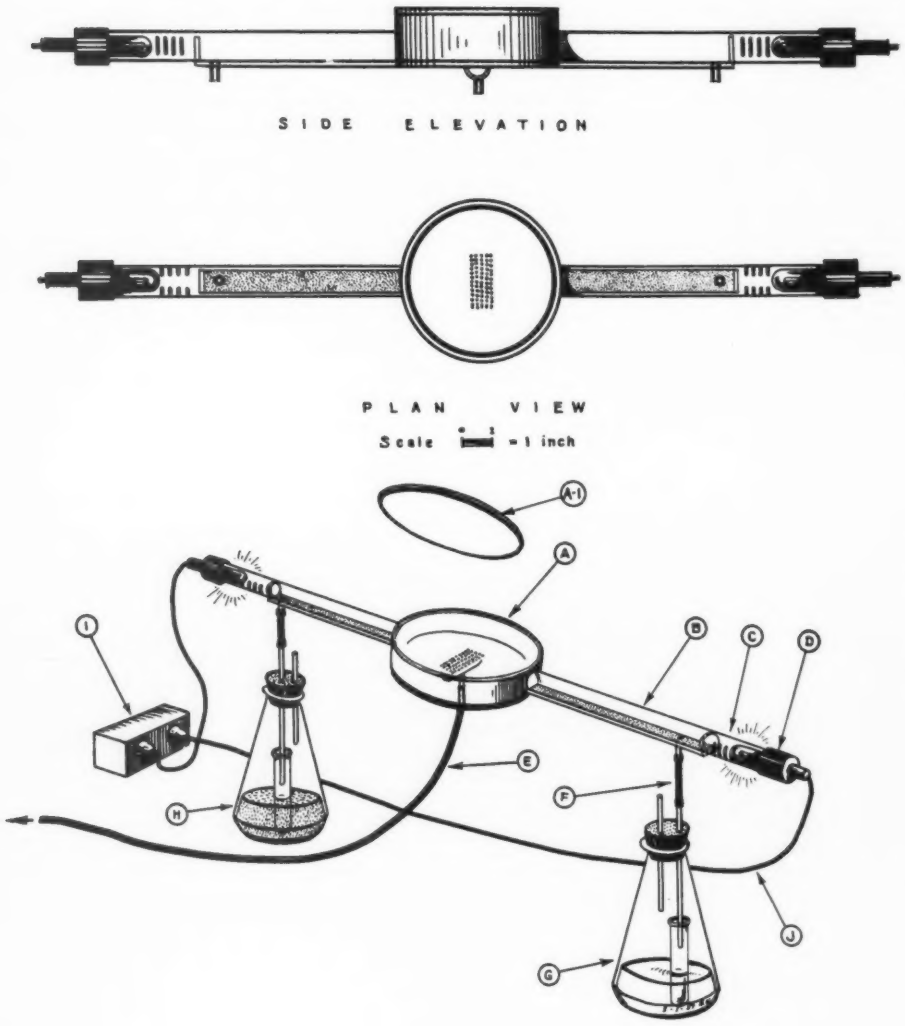

FIGURE 1. *Plan of Drum Type Plastic Olfactometer: A, Starting Chamber; A-1, Cover with rubber gasket; B, Tube with flat roughened floor; C, Light chamber and light; D, Fiber collar; E, Rubber suction tube; F, Trap tube through which beetles may fall into dry test tube; G, Erlenmeyer flask containing sterile broth; H, Erlenmeyer flask containing broth inoculated with yeast; I, Power transformer for lights; J, Electric wire to lamp socket.*

12, 13) and I run showed significant rejection of the culture (No. 5). All 3 pure cultures of *Candida mycoderma* (C_2) were very significantly rejected by the beetles. *Saccharomyces pastoria* was significantly attractive in 2 out of 3 runs. All 3 tests of beetle reaction to *Hansenula capsulata* (H) gave insignificant results. The representative test of the attractiveness of galleried bark (No. 14) gave very significant positive results; and that of fresh, uninfested bark was insignificant (No. 18).

Discussion

This pioneer study of one aspect of the ecological significance of yeasts in association with the Douglas-fir beetle indicates attractive powers of some of the yeasts. While broad conclusions are not possible on the basis of this preliminary work, some of the observations are suggestive. Techniques for the evaluation of attractant substances in relation to subcortical insects require more study. Those which have come to our attention are not satisfactory to the biological problems involved. Under experimental conditions with the new apparatus described, responses of the beetles to substances tested were indicative. The general significance of the results will be determined only by further work.

The very significant acceptance of the

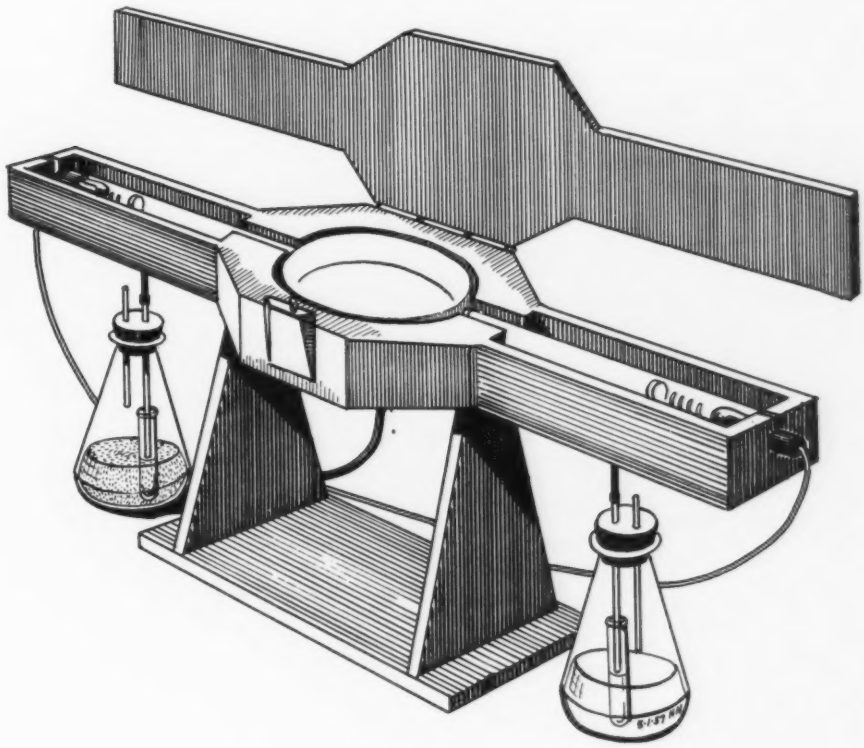

FIGURE 2. *Olfactometer Setup.*

cultures of the combined species of yeasts may be caused by the independent attractant principles of one or more species of the combination or by biochemical interaction. The answer to this may appear through chemical analysis.

Summary

1. Samples of Douglas-fir bark, both uninfested (never attacked by the beetle), and infested (containing galleries in current use) by the Douglas-fir bark beetle (*Dendroctonus pseudotsugae* Hopkins), and large numbers of adult beetles in breeding season, were collected from the east slope of the Coast Range Mountains and some from the west slope of the Cascade Mountain Range, in western Oregon, in 1953, and in 1955.
2. Cultures were made from the galleries in the bark, and from beetles (external and alimentary parts). These cultures plated out as yeasts.
3. Identification of the yeasts showed that some beetle cultures included all 4 species found associated with the Douglas-fir beetle in this study, and other beetle cultures contained pure *Saccharomyces pastoria*, *Candida parapsilosis*, *C. mycoderma*, and *Hansenula capsulata*.
4. Attractant tests were run on cultures of the yeasts, both before and after identification.
5. Analysis showed that the cultures containing all 4 species of the yeasts were very significantly attractive to the beetles, as was also the galleried bark. Pure *Candida parapsilosis*, in 3 tests, gave insignificant results, and in a fourth test was significantly rejected. In 2 out of 3 tests *Saccharomyces pastoria* was significantly attractive. Pure *Candida mycoderma*, in all 3 tests, showed very significant rejection by the beetle. Pure *Hansenula capsulata*, in 3 tests, gave insignificant results.
6. Twenty yeast isolates were obtained from 78 beetles; 13 from adults, 3 from larvae, and 4 from the alimentary tracts of dissected beetles.
7. Of the 20 isolates, 6 were sporulating forms; 4 of which were *Saccharomyces pastoria*, and 2 were *Hansenula capsulata*. The 14 non-sporulating yeasts fell into the genus *Candida*; 13 were similar to *C. parapsilosis*, and one was *C. mycoderma*.
8. The biological significance of sporulating and non-sporulating yeasts occurring in the bark beetle is not known.
9. Results of this work justify further study of the problem of host attractants and the specific responses of economically important bark infesting insects. If the ecological role of the yeasts in the life of the beetles could be established, control measures based on whether the yeasts serve as food or produce an attractive principle, could be investigated. Possibly yeast cultures could be used as baits in traps, or measures might be devised to prevent development of yeasts, especially in fallen trees.

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Russian-German Forestry Dictionary

Forstwissenschaftliches Fachwörterbuch (Scientific Forestry Dictionary) Russian-German, German-Russian. By E. Buchholz. Deutscher Verlag der Wissenschaften, Berlin (Soviet Sector). 422 pp. 1957. DM 21.90

Review by R. Stahelin
Forest Service, U. S. Department of Agriculture, Washington, D. C.

The extensive technical and scientific forestry literature published in the Soviet Union in recent years has remained largely unknown to American foresters. There is a growing feeling that the United States should keep informed of the progress made in that country. Since the excellent 850 page Russian-English-French-German forestry dictionary by Miss L. Linde, Moscow 1936, is no more available, the Russian-German and German-Russian forestry dictionary by Buchholz is a valuable help for those familiar with German.

The dictionary contains about 12,000 terms from all branches of forestry, including forest industries, as well as ecology, botany, zoology, soil science, and hunting. As indication of detail coverage it contains 33 qualifying entries for the word *nasazhdenie* (stand), 46 for the word *rubka* (cutting), and 115 for the word *les* (forest, wood). Latin names are added for all species.

Dr. Buchholz, formerly a forester in Russia, and now forest economist at the Federal Research Institute for Forestry and Forest Industries in Reinbek near Hamburg, is well known as an expert on Russian forestry by his books and numerous articles on Russian forestry in German forestry journals and in Unasylva.

Air-layering of Slash Pine

BY
P. E. HOEKSTRA

THE FIRST STEP in most forest tree improvement programs is selection of outstanding individuals. Selected trees should be propagated vegetatively to guard against losing them. Trees can be propagated asexually by grafting, rooting of cuttings, and air-layering (rooting branches while they are part of the tree). In all three methods a branch is induced to grow separately; the growing branch, called a propagule (ramet), is identical to the parent tree (ortet) in its genetic properties. External characteristics of a grafted scion may be modified by its rootstock, but cuttings and air-layers are not subject to this influence. In addition to guarding against loss, cuttings and air-layers provide one method of estimating the genotype of selections. Propagules from widely scattered selections can be assembled on a uniform site and can be compared with a standard as well as with their ortets.

Exhaustive experimentation with rooting slash pine cuttings (*Pinus elliottii* Engelm. var. *elliottii*) has not resulted in a technique by which a satisfactory percentage of plantable propagules can be obtained. Air-layering this species was first attempted in 1953 by Mergen (1955), with an encouraging degree of success. Following Mergen's exploratory work, the experiments reported here were started in 1954, to determine some of the factors that influence the rooting of air-layers. The experiments show that date of air-layering, concentration of indolebutyric acid, and, to a lesser degree, age of ortet are factors influencing the success of air-layering slash pine.

Review of Literature

Although air-layering, or marcottage, has been in use for many centuries, only a few pine species have been reported to respond successfully. In Sumatra, Lasschuit (1950) induced root formation by air-layering Merkus pine (*Pinus merkusii* Jungh. & de Vriese). Mergen (1953) added slash pine, and David (1953) added maritime pine (*Pinus pinaster* Ait.) to the list of conifers that can be propagated from marcottes.

Treatment of the wound with growth regulators (hormones) stimulates root development of some species. Hormones are applied directly to or immediately above the wound made for air-layering. They can be used in a dust, in a paste, or in solution. Mergen (1955), working with slash pine,

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This report is based on a thesis submitted to the School of Forestry, North Carolina State College, in partial fulfillment of the requirements for the degree of Master of Science.

Grateful acknowledgement is made to Dr. F. Mergen, John A. Hartford Forestry Research Center, Yale University, for his helpful suggestions in the planning and execution of this experiment, and to Dr. T. E. Maki, School of Forestry, North Carolina State College, for his constructive review of the manuscript.

used a commercial preparation of 0.8 percent indolebutyric acid in talcum powder. Average rooting percentage for treated branches was 84.6 and for untreated shoots 50.0.

Age of the ortet has a pronounced influence on the rooting capacity of tree propagules (Zimmerman and Hitchcock, 1946). As a tree grows older, it becomes more difficult to propagate vegetatively. Zimmerman and Hitchcock (1946) also found that best rooting results are obtained on current year's growth.

A more comprehensive review of the literature on air-layering can be found in Mergen's article (1955).

Experimental Materials and Methods

Two age classes of trees were selected for the 1954 tests near Lake City, Fla. Thirty-six slash pines were located in a 6-year-old plantation growing vigorously on Blanton fine sand and apparently healthy. Spacing in the plantation was 9 × 9 feet; average height and d. b. h. were 16.5 feet and 3.4 inches, respectively.

A plantation of the desired age was not available; therefore 36 trees were selected in a natural stand of slash pine. This stand grew on Leon fine sand at a density of about 100 stems per acre, and selected trees averaged 23 years in age, 56 feet in height, and 11.4 inches in d. b. h. The experimental trees were chosen with the object of keeping variations in age, diameter, crown development, and growing space to a minimum.

Indolebutyric acid was applied in concentrations of 0.4, 0.8, and 1.2 percent (by weight) in a talcum powder carrier. This hormone treatment in the form of a dust is easy to apply and has lasting effects. To prepare the dust, indolebutyric acid crystals were dissolved in a small amount of 95 percent alcohol, and this solution was stirred in talcum powder to form a paste. The paste was then dried in darkness under a fan and stirred occasionally until it became a dry powder again.

The first 360 air-layers (180 for each age class, 10 for each tree) were made in the second week of July and removed after 12 weeks. The remaining air-layers (360—180 in each age class, 10 for each tree) were made in the second week of September and left for the same length of time. There were exactly 9 weeks between the two air-layering dates.

Distal tips of branches in the upper one-third of the crown were selected for air-layering. They were first stripped of their needles at the point where rooting was desired. Then a ring of bark ½ to 1 inch wide was removed with a sharp knife. Care was taken to scrape the cambial tissue from the wounded area, to prevent callus material from bridging the wound. A small wad of moist sphagnum moss, sprinkled with about 1 gram of hormone dust, was placed around the upper rim of the girdle; thus the hormone was in direct contact with the wound. A handful of moist sphagnum moss was wrapped around the girdle, which was then covered with Airwrap[1] and secured at top and bottom with paper-covered wire. The plastic film overlapped at least 1 inch, and care was taken to leave no openings for evaporation.

The design of this study was a split plot, with 72 trees, 36 per age class, 10 air-layers per tree. The age classes, or main plots, were divided into two blocks of 18 trees each. The six possible combinations of three auxin concentrations and two application dates were applied within each block. Three trees were assigned at random to one of the six subplot treatments. Six trees, or 60 air-layers, were subjected to each treatment combination for each age class.

Although 10 air-layers were put on each tree in the experiment, several branches were broken off in a severe storm that

[1]Airwrap is a commercial product of moistureproof, gas-permeable plastic, treated with a water-soluble emulsion of nutrients, insecticide, and fungicide.

swept the experimental area and destroyed a number of air-layers. These damaged air-layers were omitted from the calculations; however, air-layers that died from too-deep girdling or from internal causes were counted as failures. The sphagnum moss in only one air-layer showed signs of drying out, even though the summer and fall of 1954 were unusually dry.

No attempt was made to determine when roots emerged because the roots are brittle and break off easily when an air-layer is opened. Several weeks before collection, however, roots could be observed through the plastic film of a number of air-layers (Fig. 1).

After the air-layers were cut down, plastic film and moss were removed and the roots were counted. Some roots were broken when the tightly packed moss was removed, and several root systems dried out during the time they were exposed for root count. This procedure was necessary for an evaluation of the root system in this test, but potting the branches with the undisturbed moss will offer a better chance for continued growth. Only roots 1 mm. and more in length were counted because some shorter protuberances have the appearance of emerging roots but consist of parenchymatous tissue (Mergen, 1955).

A record was kept of the time spent in making air-layers in this experiment. Only the time necessary to climb the trees, prepare the air-layers, and collect them was noted. Travel time was excluded.

The following year, 1955, a small-scale test with 2 hormones was made on air-layers on 10 trees in the young plantation. Concentrations of 1.2 percent and 1.6 percent indolebutyric acid and 1.2 percent naphthaleneacetic acid were applied, each on 50 air-layers. All 3 treatments were applied on each of the 10 trees, 5 of each treatment on each tree.

Results

In the 1954 tests, percentage of rooted air-layers, averaged by treatment and age class, ranged from 16.7 to 93.6 (Fig. 2). The data were transformed by the averaged angular transformation (Freeman and Tukey, 1950) and subjected to an analysis of variance. Highly significant differences between concentrations of indolebutyric acid and between dates of application were obtained. The interaction between concentration and date also proved to be significant. The difference in rooting between the two age classes was significant at the 15-percent level of probability. Lack of significance at the 5-percent level quite possibly results from a lack of sensitivity in the experimental design. The majority of reported rooting experiments show a marked superiority for younger ortets.

FIGURE 1. *Rooted air-layers on a 6-year-old slash pine. White root tips can be observed through the plastic wrap. Photo taken September 9, 1954, 9 weeks after Airwraps were applied.*

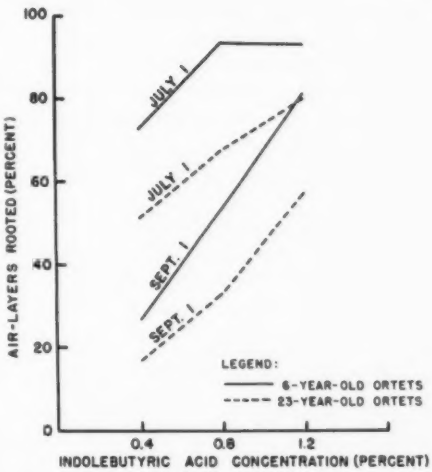

FIGURE 2. *Effect of application date, auxin concentration, and age of tree on percent rooting of slash pine air-layers.*

Evaluation of root systems on the basis of the number of primary roots (Fig. 3) strengthens and extends the rooting results previously mentioned. Number of roots per rooted air-layer, averaged by treatment and age class, ranged from 3.0 to 33.8 (Fig 4). Differences in the average number of roots per successful air-layer between dates of application and between concentrations of indolebutyric acid were highly significant. Interaction between age of ortet and date of application was highly significant, and interaction between age of ortet and concentration of indolebutyric acid was significant. From the two graphs (Figs. 2 and 4) and statistical evidence, it is apparent that the best treatment tested, with respect to rooting percentage as well as average number of roots, was application in July of 1.2 percent indolebutyric acid on the younger trees.

In the young plantation, 7.5 air-layers were prepared per man-hour. Air-layering was more time consuming on the older trees; only 3 were made per man-hour. Air-layering 23-year-old trees in midsummer with 1.2 percent indolebutyric acid resulted in 80 percent rooted branches (Fig. 2). Assuming 20 percent loss after planting, 64 percent of the attempted air-layers will become growing propagules. If this percentage is applied to the time figure obtained for the older stand, about 2 growing plants can be produced per man-hour.

In the 1955 small-scale test of hormones on air-layers on 10 trees in the young plantation, rooting percentage was 72 for 1.2 percent and 28 for 1.6 percent indolebutyric acid. Napthaleneacetic acid (1.2 percent concentration) killed 88 percent of the branches, and only 2 percent developed roots.

The lower percentage (72) of rooting

FIGURE 3. *Rooted air-layers from 6-year-old slash pine. The air-layers were made in July. The one on the left received 1.2 percent, and the one on the right 0.4 percent indolebutyric acid.*

with 1.2 percent indolebutyric acid in comparison with the results obtained the previous year can perhaps be explained by the inexperience of the persons who made the air-layers for the 1955 test. Possibly a year-to-year variation is also reflected in these results.

Planting the Rooted Branches

Fifty of the best developed and least damaged air-layers in the 1954 tests were planted in two different environments on October 8, 1954, so that subsequent growth could be observed. Ten branches from older trees and 15 branches from the young plantation were potted in 9-inch clay pots in a mixture of equal parts vermiculite and sand, and placed in a humid greenhouse. The same number of air-layers of both age classes were planted in the nursery under field conditions. All air-layers were fertilized with a soluble 7-6-19 fertiizer to stimulate growth. After 12 weeks in the greenhouse, all air-layers from the young trees and 8 from the older ortets were growing well, but 2 had died. Possibly the root systems of these 2 had dried out too much before potting. All air-layers in the nursery from both age classes had continued growth, and several of these developed male flowers. After 13 months in the field, branches from 6-year-old trees had grown an average of 3.0 feet, and air-layers from the older stand 0.9 feet.

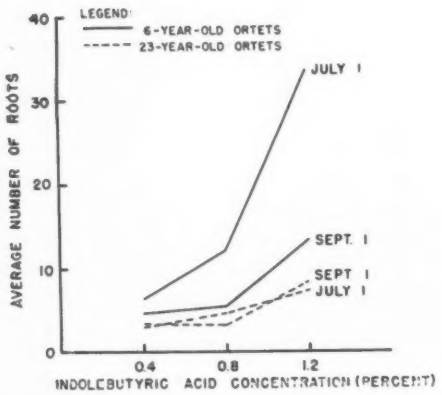

FIGURE 4. *Effect of application date, auxin concentration, and age of tree on average number of roots of slash pine air-layers.*

Discussion

The results from the 1954 tests showed that, irrespective of date of application or age of tree, 1.2 percent indolebutyric acid gave the best results with respect to percentage rooted and number of roots formed. Between the concentrations of 0.8 and 1.2 percent indolebutyric acid, the response curve in percent rooting (Fig. 2) levelled off for 6-year-old saplings air-layered in July, indicating that the optimum concentration lies somewhere in between.

The small-scale tests in 1955 showed diminished rooting response from use of indolebutyric acid in concentrations higher than 1.2. Napthaleneacetic acid (1.2 percent concentration) killed 88 percent of the branches and is not an effective hormone for air-layering.

July proved to be better for air-layering than September, though young trees still gave a satisfactory response at the later time. Gradual decrease in temperature and the approaching dormant season presumably retarded root development during the later rooting attempt. The use of this method of vegetative propagation as late as September depends largely on whether a greenhouse is available where potted branches may be kept until clement weather arrives. If no greenhouse is available, an early date of air-layering is advisable. Rooted air-layers can then be planted in the field if properly mulched, fertilized, and watered.

The present study indicates some ways to increase the efficiency of air-layering but still leaves some problems for further investigation. The ranges of age could be extended upward because many trees in tree improvement work will be much older than 23 years. It would be profitable to know the minimum size and number of

roots necessary for an air-layer to survive following different methods of planting. Possibly other hormones with other carriers should be tested to obtain better rooting for older trees.

Summary and Conclusions

During the first week of July and September 1954, indolebutyric acid in concentrations of 0.4, 0.8, and 1.2 percent (by weight) in a talcum powder carrier was used on 720 air-layers on seventy two 6- and 23-year-old slash pine trees. Increase in concentration of indolebutyric acid from 0.4 to 0.8 to 1.2 percent was associated with an increase in the number of rooted air-layers, except that no difference in response was noted between the use of 0.8 and 1.2 percent hormone when applied to 6-year-old trees during the first week of July. Increase in hormone concentration was also associated with a higher number of roots per rooted branch. Air-layering in July gave better results in number of rooted air-layers as well as number of roots per branch. Older trees treated with 1.2-percent hormone in July gave a satisfactory rooting percentage (80 percent) and average number of roots (7.5). Survival and growth of planted air-layers were as good after 12 weeks in the nursery as in the greenhouse.

In the 1955 tests 1.2 and 1.6 percent concentrations of indolebutyric acid and 1.2 percent napthaleneacetic acid were applied on 150 air-layers, 15 on each of 10 young slash pines. Rooting percentage was 72 for 1.2 percent and 28 for 1.6 percent indolebutyric acid, but only 2 percent for 1.2 percent napthaleneacetic acid. The latter acid killed 88 percent of the branches.

July is a better time than September for making air-layers on slash pine. Air-layers can be made on young trees in September if a greenhouse is available for protection of the potted plants over winter. Indolebutyric acid (1.2 percent) is effective in promoting root formation and growth.

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New Forestry Terminology

Forestry Terminology, the last edition of which was issued in 1950, has been revised and is now in press. It should be available early in 1958 from the Society of American Foresters, Mills Bldg., Washington, D. C.

A Method for Measuring Transpiration of Intact Plants Under Controlled Light, Humidity, and Temperature

BY
JOHN P. DECKER
BARTON F. WETZEL

NUMEROUS ATTEMPTS have been made to study transpiration by the vapor-production method, that is, by enclosing a part of a plant in a transparent chamber and measuring the resulting increase of humidity. According to Maximov (1929), the first such study was made by Guettard in 1748. More recent work has been reviewed by Crafts *et al.* (1949). Although the vapor-production method has the advantage of permitting studies on undisturbed plants growing in natural situations, its use has been limited by lack of a practical means of measuring rapid changes of humidity. Andersson *et al.* (1954) have reported transpiration studies in which a corona discharge device served as a hygrometer, but this device would be difficult to adapt to field studies.

In the method described here, an infrared gas analyzer (Liston-Becker model 15A) served as a sensitive and fast-acting hygrometer. The present apparatus was designed for laboratory use with potted plants. It was intended as a prototype for apparatus to be used for measuring comparative transpiration rates of forest species in the field, especially phreatophytes. These water-loving plants grow mainly along stream courses, where their roots reach into the capillary fringe overlying the water table (Fletcher and Elmendorf, 1955).

Apparatus and Procedure

The apparatus is similar to one used for measuring photosynthesis of tree seedlings (Decker, 1954) and is shown diagrammatically in Figure 1. The shoot chamber was a plexiglas-topped cylinder of sheet iron that rested on a brass base plate. The chamber was assembled around the shoot, and all joints were sealed with modeling clay. The shoot chamber, hygrometer, and an air pump were in closed series connected with plastic tubing and ground glass joints. Air circulated continuously between chamber and hygrometer. Time required for the plant to produce a given amount of water vapor was measured. Rate of transpiration was calculated from these data.

A calibration curve, based on four points, was made for the hygrometer. Zero was set as the equilibrium reading for air recycled through a closed system consisting of

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The authors are, respectively, Plant Physiologist and Forestry Aide, Rocky Mountain Forest and Range Experiment Station, Forest Service, U. S. Department of Agriculture; general headquarters of the station are maintained at Ft. Collins, Colo., in cooperation with Colorado State University. The research reported here was done at Tempe, Ariz., in cooperation with the University of Arizona and Arizona State College.

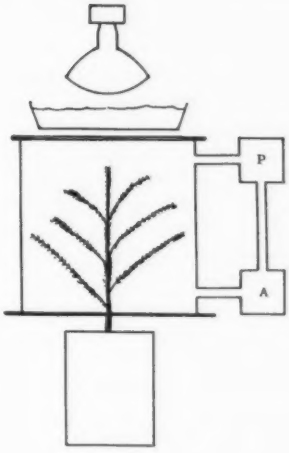

FIGURE 1. *Diagram of the transpiration apparatus. Entire shoot is sealed in chamber and is illuminated from above. The pump and analyzer are represented by P and A, respectively.*

the hygrometer, pump, and a series of three drying tubes charged respectively with Drierite, Ascarite, and Anhydrone. Drierite was used as a convenient preliminary desiccant. Ascarite was included to remove carbon dioxide, to which the hygrometer was slightly sensitive. According to Diehl and Smith (1952), the residual humidity over Anhydrone is 0.0001 mg./liter.

Next, the sensitivity of the hygrometer was adjusted so that the equilibrium reading for air recycled through a bubbler of distilled water held in a water bath at 20° ± .01° C. was full scale. To minimize temperature change of the distilled water during the bubbling, the air was passed through a loop of copper tubing immersed in the same water bath before it entered the bubbler. Two intermediate readings were obtained with similar bubblers of saturated aqueous sodium acetate and potassium acetate. According to the vapor pressures given by Hodgman (1945), the latter three humidities were, respectively, 17.26, 13.02, and 3.42 mg./liter. In routine operation, the hygrometer was checked against the zero and full-scale standards about once each hour.

Transpiration could not be calculated simply as the product of a change of humidity multiplied by the volume of the system. Surface adsorption effects were so large that calculations of transpiration based on the gas phase alone were unreliable. Accordingly, the apparatus was calibrated directly in terms of the amount of water required to produce a given change of humidity. The hygrometer, pump, and empty chamber were coupled in closed series. Humidity was adjusted by diluting the contained air with small amounts of wetter or drier air until the hygrometer indicated the desired reading. The pump was stopped, and a weighed, stoppered flask fitted with inlet and outlet tubes and containing a small amount of water was inserted in series between the hygrometer and chamber. The pump was run until evaporation from the flask gave the desired increase of humidity. Then the pump was stopped, and the flask was removed and reweighed. Six runs were made at each of the nine combinations of three humidity intervals and three temperatures (4.4–6.4, 8.4–10.4, and 12.4–13.6 milligrams of water per liter of air, at 30°, 35°, and 40° C.). Calibration varied with temperature and with humidity. For example, to increase the humidity of the 17.5 liter system over the 12.4–13.6 interval required 35.9 milligrams of water at 30°, 27.4 at 35°, and 23.5 at 40° C.

The calibration is for the empty chamber and does not take into account possible surface adsorption on the plant itself. If this were appreciable, it would be a source of unevaluated error, which would probably cause measurements at low temperature and at high humidity to appear somewhat too low.

Illumination was provided by a 300-watt internal-reflector floodlamp focused on the chamber through a heat filter of distilled water in a glass dish. The distilled water was cooled by a loop of copper tub-

ing through which tapwater flowed. Illumination was varied by inserting up to five sheets of white bond paper between the heat filter and chamber top. Intensities were measured with a light meter (Weston model 756), with the target held horizontally in a position about equivalent to the midpoint of the crowns of the seedlings.

Air temperature within the chamber was controlled in two stages. The main heating or cooling load was carried by the wall of the shoot chamber, which was wrapped externally with copper tubing. Water of a constant temperature was pumped through the tubing as the first stage of temperature control. The final, more delicate control was automatic. The thermoregulator was a 0.1° C. thermometer to which was attached a Thermocap relay that controlled a small water pump. The pump forced water through a heat exchanger (a coil of copper tubing and a small electric fan) mounted inside the chamber. With careful balancing of heat loads, air temperature within the chamber could be held within 0.05° C. Preliminary work showed that temperature control to within only 0.5° gave erratic results.

A close control of humidity was inherent with the procedure used. Each observation of transpiration was made by timing the increase of humidity across a fixed interval. Mean humidity for that observation was thus fixed as the midpoint of the interval.

Air in the chamber was stirred at an apparently constant rate by the small radial-flow fan of the heat exchanger unit. The turbulence caused a mild flutter of small twigs. Precise temperature control could not be achieved without the fan, and thus a study of the effect of lower wind velocity was not practical.

The routine operating procedure was as follows: The shoot was sealed in the chamber and left for 30 minutes under full light before measurements of transpiration were begun. During this period the chamber was tested for leaks by connecting it temporarily to an infrared carbon dioxide analyzer and flooding all joints with carbon dioxide. Small leaks were detected readily in this way. Before a transpiration measurement was made, the chamber was ventilated with dry compressed air introduced through a hole in the side wall. When the hygrometer reading was conveniently low, the ventilating tube was removed, and the hole was plugged with a rubber stopper. The hygrometer reading began to increase a few seconds after ventilation was stopped. The increase was timed across the desired intervals, and the procedure was repeated as needed.

Effect of Light Intensity

Six potted seedlings of five-stamen tamarisk (*Tamarix pentandra* Pall.) were used. They were 20–40 centimeters high and had grown in a greenhouse in 1-gallon cans containing clay soil. They were transplanted to the cans as small seedlings (10-20 millimeters high) dug from the banks of the Gila River near Phoenix, Ariz. The soil remained moist throughout the experiments.

All observations were made at 35° C. and at a mean absolute humidity of 9.4 milligrams per liter. A typical seedling transpired 33 milligrams in about 25 seconds at 3,000 foot-candles.

Six light intensities were run in a sequence of descending order. Triplicate observations were made at each light intensity. The triplicates were pooled and the analysis of variance was based on 36 means (6 plants × 6 intensities). The results are shown in Figure 2. The confidence range shown is based on the error term of the analysis of variance (plant-intensity interaction). Because all plants received all intensities, the amount of foliage involved was constant and did not affect comparisons between intensities.

Transpiration increased nearly linearly with light intensity up to at least 600 foot-candles. Light saturation began between 600 and 3,000 foot-candles.

To test the method further, the study was repeated with another species. Six seedlings of Arizona cypress (*Cupressus*

arizonica Greene) were used. These plants were obtained from a commercial nursery; they were in 1-gallon cans containing clay soil and were 30–40 centimeters tall. The experimental procedure was the same as that used with tamarisk, and the results were essentially the same, the transpiration curve being nearly the same shape as that in Figure 2 but somewhat less steep.

Because tamarisk is typically a phreatophyte and Arizona cypress typically a mesophyte, a direct comparison of their transpiration rates would be interesting. Unfortunately, such a comparison is very difficult because of lack of a meaningful denominator. The usual denominator, amount of foliage, can be misleading (Decker, 1955) and with these species, foliage is impractical to measure. However, it was noteworthy that although the cypress seedlings were conspicuously larger, with much denser crowns and apparently several times more foliage than the tamarisk seedlings, average transpiration rates (on a per shoot basis) at high light intensity were nearly the same.

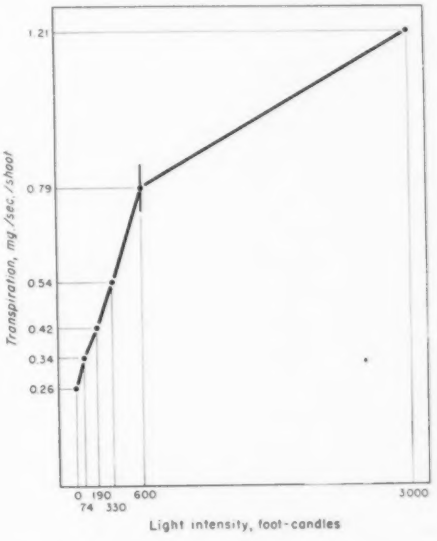

FIGURE 2. *Effect of light intensity on transpiration of five-stamen tamarisk at constant temperature (35°C.) and constant humidity (9.4 milligrams per liter). Each point is the mean of 18 observations. Confidence range is 5% tse (t × standard error of mean).*

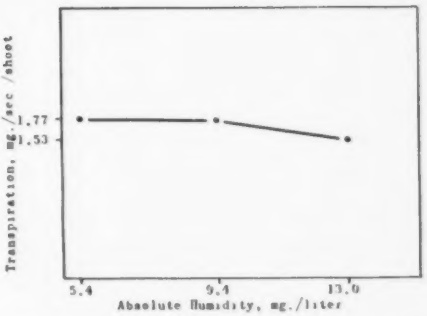

FIGURE 3. *Effect of humidity on transpiration of tamarisk at a mean temperature of 35°C. and constant light intensity (3,000 foot-candles). Each point is the mean of 36 observations. 5% tse (± .026) is included within the dot.*

Effect of Temperature and Humidity

The same six tamarisk seedlings were used in a study of the effects of temperature and humidity on transpiration under constant illumination. Observations at three humidities were taken in close succession as humidity increased over three successive ranges, 4.4–6.4, 8.4–10.4, and 12.4–13.6 milligrams per liter. The chamber was ventilated and the series repeated immediately. Three such series were run at 30°, 35°, and 40°C. with each plant. Thus, there were 18 replications of the humidity series and 6 replications of the temperature series. This gave two orders of precision in the analysis of variance.

The results are graphed in Figures 3 and 4. All differences are statistically significant except the slight one between the upper two points of Figure 3. Transpiration decreased with humidity and increased with temperature in accordance with the

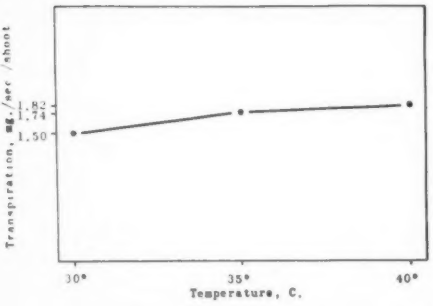

FIGURE 4. *Effect of temperature on transpiration of tamarisk at a mean humidity of 9.3 milligrams per liter and constant light intensity (3,000 foot-candles). Each point is the mean of 36 observations. 5% tse (± .037) is included within the dot.*

general principles outlined by Meyer and Anderson (1939).

Summary

A laboratory method has been developed for measuring transpiration of potted plants under controlled light, humidity, and temperature. An infrared gas analyzer (Liston-Becker model 15A) serves as a sensitive and fast-acting hygrometer. This method was tested on potted seedlings of five-stamen tamarisk and Arizona cypress. Transpiration rate increased as light intensity and temperature increased; rate decreased with rising humidity. Work is under way to adapt this method to field use.

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Male Flowers on One-Year-Old Mugo Pine Seedlings

BY
FRANCOIS MERGEN
STEPHEN G. CUTTING

IT IS GENERALLY ASSUMED that forest trees, and conifers in particular, do not flower in the seedling stage. The opinion has also been expressed that trees which flower at a precocious age produce reproductive organs which are infertile. Reported here are observations on the production of viable pollen by pine seedlings less than one year old.

A record of early flowering among 57 species or varieties of pines grown at Placerville, California was published by Righter.[1] The average minimum age was 4.4 years for staminate flowers, and 5.2 years for ovulate flowers. One species, Chinese pine *Pinus sinensis* (*P. tabuleformis*, Carr.), bore male flowers during the first year. Another instance of male flower production on a 15-month-old Mugo pine, *Pinus montana* (*P. Mugo* Turra), seedling was reported by Hermann.[2] In this second instance, however, the male flower was possibly the result of heteroplastic micrografting; as he had grafted the *Pinus montana* seedling onto understock of Scotch pine, *Picea excelsa* L.

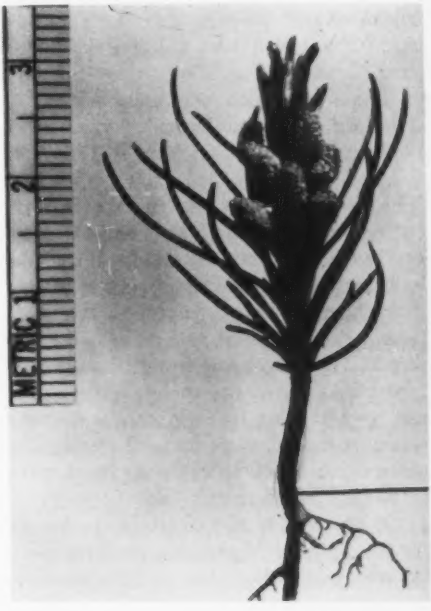

FIGURE 1. *Staminate flowers on an eleven-month-old Mugo pine seedling. The secondary needles which start to form above the catkins are still enclosed in their sheaths.*

[1]Righter, F. I. 1939. Early flower production among the pines. J. For. 37:935-938.

[2]Hermann, S. 1951. Im Primärstadium blühende Kiefer. Naturwissenschaften 38 (16): 381-382.

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In the spring of 1957, staminate flowers were observed on Mugo pine seedlings, *Pinus Mugo* var. *Mughus* (Scop.) Zenari (dwarf type), that were less than 1 year old (Fig. 1). Three seedlings, from a total of about 330, bore respectively 12, 6, and 4 catkins. The catkins were of normal size and the seedlings shed their pollen at the same time as older Mugo pine trees in this area did.

Pollen appeared similar in shape and size to that from older Mugo pine trees. The air-sacs had developed normally and the nuclear divisions within the microspore had progressed through to the formation of the antheridial nucleus. Both percentage germination and tube growth were normal when the pollen was cultured in double distilled water (Fig. 2).

The seed which was collected in the Tyrolean Alps, was broadcast-sown in an outdoor nursery bed on May 3, 1956. By the end of June it had fully germinated. The seedlings received no special treatment, but received adequate water, and the nursery bed was weeded by hand, rather than by chemical means. It is of interest to note that these seedlings developed staminate strobili before secondary needles were laid down. The secondary needles started to form right above the male catkins. One can assume that the primordia for the staminate strobili were initiated during late summer, at which time the seedlings were between 2 and 3 months old.

Of 86 seedlots of 1-year-old conifers in the nursery, the Mugo pine seedlings were the only ones which flowered during their first year. However, there was a large number of 3-year-old pines in field plantings which had both staminate and pistillate flowers. Heavy flowering was especially pronounced in the *Lariciones* (Shaw) group. Because so far all of the reports on early flowering for pines were for members in the *Lariciones* group it appears that species within this group might be well adapted for investigations on early flower induction in pine.

FIGURE 2. *Germinated pollen grain. The generative and tube nuclei are still inside the main body of the microspore.*

Embryo Dormancy and Embryo Vigor of Sugar Pine as Affected by Length of Storage and Storage Temperatures

BY
EDWARD C. STONE

STORAGE AND THE SUBSEQUENT longevity of forest tree seeds have been investigated for at least a hundred years and have been subjects of general speculation for many more (Lindley, 1843). Seed longevity readily appeals to the imagination and consequently generates considerable popular enthusiasm. As a result the pertinent literature must be evaluated carefully and with caution. Ewart (1908) was impressed by this situation almost 50 years ago when in commenting on the longevity of seeds he said, ". . . a grain of truth buried in a mass of inaccuracy."

Among the forest trees some produce seeds that store well while others produce seeds that store poorly. At one end of the scale is *Cassia multijuga* Rich. whose seeds germinate well after 150 years of room temperature storage (Becquerel, 1934). At the other extreme is black willow, *Salix nigra* Marsh., whose seeds lose their viability after only a few days of storage (Tillotson, 1921a).

The most optimistic report of seed longevity among the conifers is made by Mills (1915) for lodgepole pine, *Pinus contorta* Dougl., growing in the Rocky Mountains. In that particular area *Pinus contorta* has persistent cones that often become buried in the woody tissue as a result of normal cambial growth over the years. From the ring counts and the depth of the cones buried in a board cut from one of these trees, Mills concluded that the viable seeds he obtained from these buried cones were at least 150 years old. This report has yet to be substantiated by subsequent work. However, several years previously Coker (1909) and Blumer (1910) had found viable seeds in *Pinus contorta* cones up to 30 years old.

During the last 20 years many reports on the germination behavior of stored pine seeds have appeared (Latour, 1942; Mirov, 1936a, 1946; Nelson, 1940; Roe, 1948; Schubert, 1952, 1955b; Tiren, 1942; Uebersezig, 1947). Although not in close agreement on many points, they do indicate that seeds of some pine species store well under a variety of conditions,

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e.g., Monterey pine, *Pinus radiata* D. Don, while others do not, e.g., sugar pine, *Pinus lambertiana* Dougl.

Unquestionably, many of the conflicting reports on germination behavior are the direct result of different storage methods. For example, storage in sealed containers, as first explored by Cieslar (1897), gives different results than open storage. Furthermore, the storage temperature, the moisture content of the seeds, and the relative humidity of the atmosphere surrounding the seeds affect the capacity of the seeds to withstand prolonged storage (Barton and Crocker, 1948; Dybeck, 1923; Haack, 1909; Heit and Eliason, 1940; Tillotson, 1921b).

In addition to the storage environment and the storage period, many other more or less obscure factors have been reported as affecting pine seed germination. Necessarily these factors are important in assessing the effect of any particular storage treatment. Therefore, in order to place the present study in its proper perspective, some review of these factors is essential.

First there is the question of seed origin. Both Schmidt (1930) and Wiebek (1931) reported that seeds of Scotch pine (*Pinus silvestris* L.), collected from trees growing in several different regions, had different rates of germination. Koblet (1932) reported the same to be true for eastern white pine (*Pinus strobus* L.) and Pearson (1914) reported similarly for ponderosa pine (*Pinus ponderosa* Dougl.).

Regarding the effect of the age and vigor of the parent tree there is considerable difference of opinion. Holmerz (1900), Busse (1937), and Green (1920), reported that seeds from young trees of *Pinus silvestris* had a higher germination capacity than seeds from older trees. On the other hand, Schotte (1914), working with the same species, and Olson (1932), working with *Pinus ponderosa* and western white pine (*Pinus monticola* Dougl.), failed to find any correlation between parent age and germination capacity.

Apparently, the effect of cone size on seed germination is important for some species, but not for others. For example, Giersten (1904), working with *Pinus silvestris*, Dimitroff (1926) working with Balkan pine (*Pinus peuce* Griseb.), and Perry and Coover (1933) working with shortleaf pine (*Pinus echinata* Mill.), all reported good correlation between cone size and germination capacity. However, when Perry and Coover (1933) investigated pitch pine (*Pinus rigida* Mill.) they failed to find such a relationship.

The picture is further complicated by the conflicting reports that the position of the seed in the cone and the position of the cone on the tree affects its subsequent germination. For example, Munns (1921) reported that Jeffrey pine (*pinus jeffreyi* Grev. & Balf.) seeds from the lower portion of the cone had a faster germination rate than seeds from the upper portion, while McIntyre (1919) did not find this to be true with Table-Mountain pine (*Pinus pungens* Lamb.). Acatay (1938) working with *Pinus silvestris* reported a higher germination capacity of seeds from cones near the base of the crown while Perry and Coover (1933) were unable to find any difference in the germination capacity of seeds from the top and bottom of the crown of *Pinus rigida*.

Superimposed upon these relationships is the reported effect of seed color. Hessilenk (1922) and Seitz (1927) working with *Pinus silvestris*, Dimitroff (1926) working with *Pinus peuce* and Perry and Coover (1933) working with *Pinus echinata*, found that dark colored seeds germinate better than light colored seeds. On the other hand, Pittauer (1914), while studying Austrian pine (*Pinus nigra* Arnold) and Zemis (1928) while studying *Pinus silvestris*, found that light colored seeds germinated better than dark colored seeds provided they had been stored for at least one year.

Maki (1940), working with *Pinus ponderosa* and Fowells (1949) working with *Pinus lambertiana*, found that the specific gravity of the cone, which is an indica-

tion of its ripeness, has a pronounced effect upon seed germination. Schubert (1955a) agreed with these conclusions. However, in addition he found that, after one year of cold storage, germination of *Pinus lambertiana* seeds from cones which had a specific gravity of .90 or higher when collected, decreased almost to zero while the germination of seeds from cones which had a specific gravity of .80 or less when collected germinated well after one year of cold storage.

Finally, there are the reports of an internal germination rhythm within the seed itself. According to Schmidt (1930), who worked with *Pinus silvestris*, and David (1951), who worked with cluster pine (*Pinus pinaster* Ait.), the germination rate and the germination capacity varied in the same lot of seed in the course of a year, even though germination temperatures were controlled. Each spring a surge of especially rapid germination apparently occurred, while each winter it apparently declined to a minimum level.

Thus, even though many of the above reports may not be entirely reliable, they at least indicate that there are many factors that can affect the storing ability and consequent longevity of the pine seed.

In addition to the initial germination of the seed, the embryo vigor—the vigor with which the seedling develops—is apparently affected by storage of the seed. Haack (1912) was one of the first to report this effect and developed the concept of the "plant percent" as opposed to the germination percent. "Plant percent" is the number of seedlings that become established, per 100 seeds planted in the seed bed, and excludes those seeds that germinate, but whose hypocotyl elongation is insufficient to push the cotyledons above the ground or whose radicles fail to elongate sufficiently for the seedling to survive after germination. Tiren (1945), has found that the plant percent in *Pinus silvestris* decreases as the seed ages while the germination percent may still remain high. With Norway spruce (*Picea abies* Mill.), on the other hand, he found that a decrease in the plant percent is generally reflected in a concomitant decrease in the germination percent. Dyachenko (1940) reported that the plant percent as well as the germination percent of *Pinus strobus, Pinus ponderosa, Pinus rigida, Pinus contorta* and *Pinus peuce* can be increased by stratification. Since many workers have not made the distinction between "germination percent" and "plant percent" additional confusion has developed in a field already in confusion.

The next question that logically follows is, "What happens during storage that alters the 'germination percent' and the 'plant percent'?" Many investigators have followed chemical changes during seed storage; see the review by Miller (1938). Most investigators working with pine seeds have been impressed by changes in the chemical composition of the fats during storage (David, 1951; Goksin, 1942; Mirov, 1944; Vincent, 1929). Nevertheless, today the biochemical cause of aging is still to be unravelled. Why the seed from one species of pine stores well while that from another one does not, is yet to be explained.

The dormancy of a very large number of temperate zone seeds that respond favorably to stratification can also be overcome by breaking or removing the seed coats. This has generally been interpreted as indicating non-dormant embryos, and the pines have been placed in this category (Crocker, 1948; Crocker and Barton, 1953; Miller, 1938; Wakeley, 1931). However, Stone and Duffield (1950) found that under certain conditions the embryo of *Pinus lambertiana* was at least partially dormant. This was apparent when they attempted to use their modified embryo culture technique on stored as well as freshly harvested seeds.

An attempt by the author in 1949 to evaluate conflicting reports by Mirov (1936b), Haddock (1942), and Stone (1948), regarding auxin change during

stratification[1] of *Pinus lambertiana* seed was only partially successful. Auxin changes did occur during stratification, but they varied from one seed lot to the next. It was obvious that "standardized" seed was needed. Therefore, the following year a large quantity of seed was collected from one tree, dried to a moisture content of 10 percent, and then stored at 5° C. in sealed containers. But even this uniformly treated seed could not be considered "standardized," because germination behavior changed considerably during the first 12 months of storage. It became important, therefore, to obtain more specific information about germination behavior prior to the continuation of the auxin studies. Consequently, a series of germination behavior studies were undertaken. Part of the results have been published elsewhere (Stone, 1957). The data to follow were collected over a 5-year period and have been organized so as to show, in particular, the effect storage has on germination and the effect stratification has on "rejuvenating" stored seed.

In addition to studies on germination behavior, others dealing with embryo vigor are also reported, where elongation of the radicle and hypocotyl following germination was used as a measure of vigor. These studies were included, because it was found that, in *Pinus lambertiana* at least, seed age, as well as storage conditions, was often more clearly reflected by the vigor of the embryo than by the initial appearance of the radicle which constitutes germination.

Materials and Methods

Seeds used. The seeds used in these studies were from three different seed lots. Lot 36 was collected by the U. S. Forest Service on the Sierra National Forest in 1936. After the seeds were air dried and cleaned, they were stored at 5° C. in air-tight containers until used. When removed for use after 17 years, the average moisture content was 11.3-percent. Lot 49 was collected by the U. S. Forest Service from one tree near Placerville, Calif., in 1949. The seeds were air dried, cleaned and then stored at 5° C. over $CaCl_2$ in a sealed glass jar. The average moisture content of the seeds when removed from storage was 8.6-percent. Lot 53 was collected by the author from 5 trees on a ridge near Placerville, California. Some cones were kept separate and the seeds removed from the cones before drying by tearing off the scales with a pair of pliers. The rest of the cones were dried in an oven at 50° C. ±2° C. until the scales opened. Then the seeds were shaken out, dewinged by rubbing between the hands, and dried at room temperature until the average moisture content was reduced to approximately 10-percent. The seeds were then cleaned by running them through a clipper seed separator after which they were stored over $CaCl_2$ in closed desiccators. Most of the seeds were stored at 2° C.; however, a small quantities were stored at −18° C. and at +25° C. The seeds that had been removed from the green cones by tearing off the scales, were dried at 30° C. ±1° C. until the moisture content was reduced to approximately 8-percent. After dewinging and cleaning they were stored at 1° C. over $CaCl_2$ in sealed jars until used. The specific gravity was determined for 200 out of a total of 550 cones. It varied from .60 to .94, with 90-percent of the cones having a specific gravity of less than .85.

Stratification. Stratification consisted of mixing the seeds with wet vermiculite, pouring the mixture into pint-size ice cream cartons, sealing the cartons and then storing them in a cold room at 5° C. for 3 months.

Sample size and statistical treatment. Initially, 5 samples of 10 seeds each or a total of 50 seeds were used to establish the germination curves. This was sufficient in all cases to establish the relative position of the

[1]Stratification as used here refers to cold storage of seed at 5° C. in a moist aerated medium such as damp sand or peat moss for a period of three months before planting.

curves. However, with this limited number of seeds, smooth curves could not be drawn in several cases when older seeds were used since germination was slow and irregular. When the number of samples was increased to 15, giving a total of 150 seeds per treatment, the fit of the curves was good and entirely adequate.

All curves except those in Figure 3, are based on data from 15 samples of 10 seeeds each. The data plotted herein are based on 100 seeds from each cone, 50 being germinated after stratification and 50 before. The limited number of seeds per cone in this case restricted the sample size; however, since the objective was to show the variation in seed germination from different cones, the number of seeds was considered sufficient.

The relative positions of the curves remained the same when the first 5 samples of 10 seeds each were plotted separately, when the next 5 samples were plotted separately, and when the last 5 samples were plotted separately. Thus there is reasonable assurance that the relative position of the germination curves shown in the figures are reliable. In most cases the germination of each of the 5 samples of 10 seeds each was carried out at different times. Thus they included any variation in the germination technique that might normally occur on a day-to-day basis.

Where specific comparisons were made of points on these curves the standard error of the difference of the means was calculated and the t-test used to determine whether or not the differences were significant (.05 level). Since comparisons were made of the number of days for germination to begin or to reach some particular level, i.e. 50-percent, transformation of the percentage data before performing the t-test was not required.

Germination. Whole seeds were germinated in petri dishes filled with wet vermiculite, as described earlier (Stone, 1957). Seeds from which the seed coats, papery membranes and nucellar remains had been removed were germinated on agar in individual culture tubes as described earlier (Stone, 1957). Again, the earliest visible external manifestation of embryo growth, which was the first appearance of the radicle, was used as the basis for determining germination. An interesting point in this regard was the considerable amount of false germination that occurred at the lower germination temperatures when the seed coats were removed. Often, and as long as two months before the radicle appeared, the "rootcap" swelled and protruded.

Germination was carried on in incubators held within $\pm 0.5^\circ$ C. of the selected temperature. Light was excluded except for the few minutes required each day to record germination and make measurements.

Embryo vigor. Radicle and hypocotyl elongation measurements were made only on seedlings growing on agar and were accomplished by laying a ruler along the outside of the culture tube and visually projecting the root onto the ruler. There was some error in this method of measurement, but it was not of any particular importance in this study because of the large differences resulting between treatments.

The number of days for the radicle to reach 3 inches, when the seedling was kept in the dark, was used as a measure of radicle activity. Three inches was used, because it showed most clearly the effect of temperature of storage, although 2 inches or even 1 inch would have been sufficient. For a similar reason, the number of days for the hypocotyl to reach 3 inches was used as a criterion of hypocotyl activity following germination.

Results

Germination of whole seeds. Unstratified seeds germinated slowly and incompletely at both 25° C. and 15° C. (Fig. 1). At 25° C., the 1-year-old seeds failed to germinate during the first 50 days and only 28-percent had germinated after 150 days. At

15° C., germination began after 60 days and 22-percent had germinated after 150 days.

When the germination temperature was maintained at 5° C., there was no germination during the first 100 days; then during the next 30 days 90-percent of the seeds germinated (Fig. 1). This delay, followed by rapid germination, would appear to be the result of stratification during the first 100 days. For the unstratified seed the germination curve at 5° C. is the same as for stratified seed except that it is displaced to the right on the x-axis a distance representing approximately 3 months. This would be expected since exposure for 3 months at 5° C. in a moist medium is a common method for stratifying pine seed.

Unstratified 1-year-old seeds germinated more slowly and had a lower germination capacity than freshly dried 1-month-old seeds (Fig. 2). One-year-old seeds started to germinate after 50 days and germination was essentially complete in 90 days with 26 percent germinated. One-month-old seeds started to germinate after 18 days and germination was essentially complete in 50 days with 38-percent germinated (difference significant at the .05 level). On the other hand, when 1-year-old and 1-month-old seeds were stratified, their germination behavior was the same. In both cases it was rapid and essentially complete with 90-percent germinated in 12 days.

By germinating the unstratified seeds from individual cones in separate petri dishes, both the germination rate and the germination capacity of seeds from different cones were found to vary over a wide range (Fig. 3). For example, although seeds from cone 80 and cone 97, each with a specific gravity of .70 when collected, started germination after 15 days, only 32 percent of the seeds from cone 80 had germinated after 90 days while 80-percent of the seeds from cone 97 had germinated after 40 days (difference significant at the .05 level). When the seeds were stratified a different picture developed. The seeds germinated rapidly and germination was essentially complete with 90-percent germinated in 15 days.

Thus, we see that the germination of unstratified whole seed is affected by both the age of the seed and the cone from which it comes. We also see that the effect of both these factors is minimized by stratification.

Germination of seeds from which the seed coats and papery membranes were removed. Germination is considerably improved by removing the seed coat and papery membrane. At 25° C. it is almost as effective as stratification (Fig. 4). For example, the 50-percent level of germination[2] is reached in 8 days when the seed coats and papery membranes are removed and in 5 days when the seeds are stratified. However, as the germination temperature is lowered, seed coat removal becomes much less effective than stratification in promoting rapid germination. At 10° C., the 50-percent level of germination is reached in 22 days by removal of the seed coats and papery membranes and in 7 days by using whole stratified seeds (Fig. 5). At 5° C., the 50-percent level is reached in 108 days by removal of the seed coat and papery membrane and in 28 days by using whole stratified seeds. Thus at 25° C., there is a 3-day difference in the two treatments, at 10° C., a 15-day difference and at 5° C., an 80-day difference (differences all significant at the .05 level).

As noted in Figure 2, storage affected the subsequent germination behavior of intact seeds. However, these differences in germination which resulted from seed storage, were more clearly shown by germinating unstratified seeds after the seed coats and papery membranes had been removed (Fig. 6). At 25° C., the 50-percent germination level was reached in 2 days with 1-month-old seeds, in 4 days with 6-month-old seeds, in 8 days with 20-

[2]The fifty percent level of germination is reached when 50-percent of the total seed sample has germinated. In instances where older seed was used it was never reached.

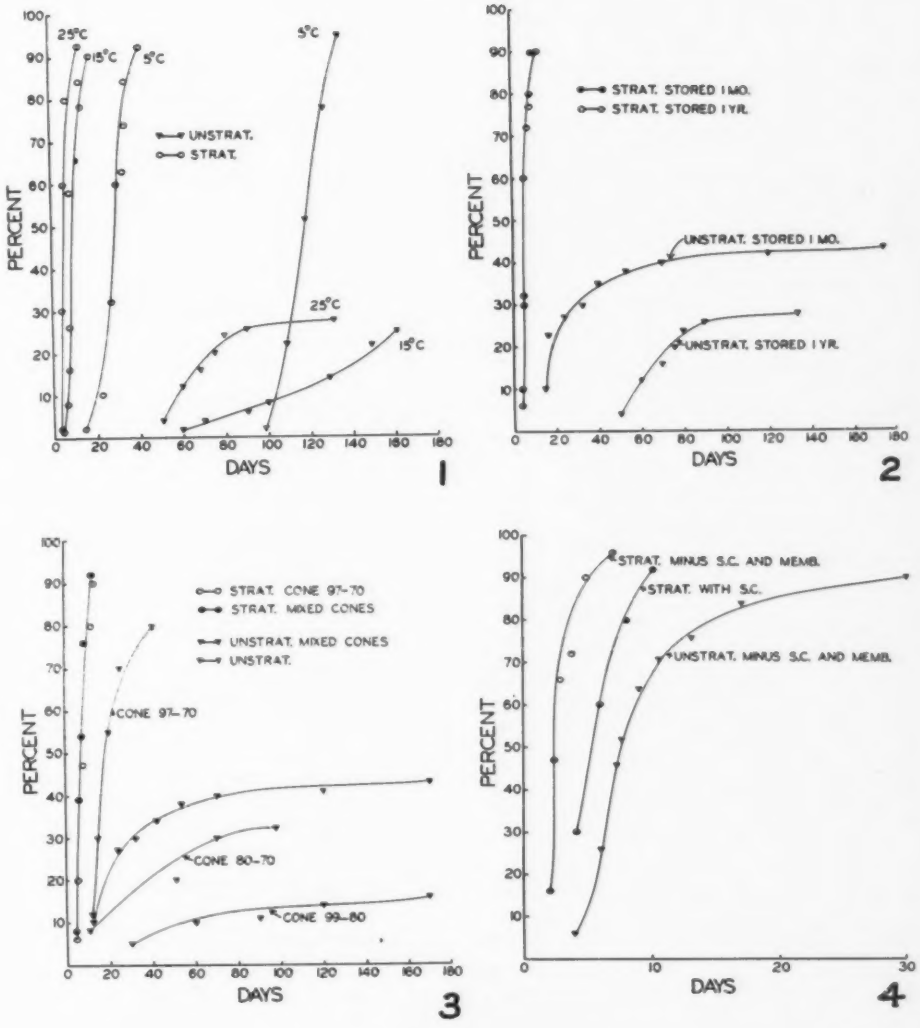


FIGURE 1. *Effect of stratification on subsequent germination at 5° C., 15° C., and 25° C. of intact seeds. (Seeds from lot 49 and stored dry at 2° C. for 1 year.)* FIGURE 2. *Effect of dry storage at 2° C. on the subsequent germination at 25° C. of stratified and unstratified intact seeds. (Seeds stored 1 year were from lot 49, and those stored 1 month from lot 53.)* FIGURE 3. *Variation in germination at 25° C. of stratified and unstratified intact seeds from randomly selected cones from the same tree. (Seeds from lot 53 had been stored dry at 2° C. for 1 month prior to use; specific gravity of each cone is indicated by the second number, i.e., Cone 80—70 has a specific gravity of .70.)* FIGURE 4. *Effect of seed coat and papery membrane on germination at 25° C. of stratified and unstratified seeds. (Seeds from lot 53 had been stored dry at 2° C. for 20 months prior to use.)*

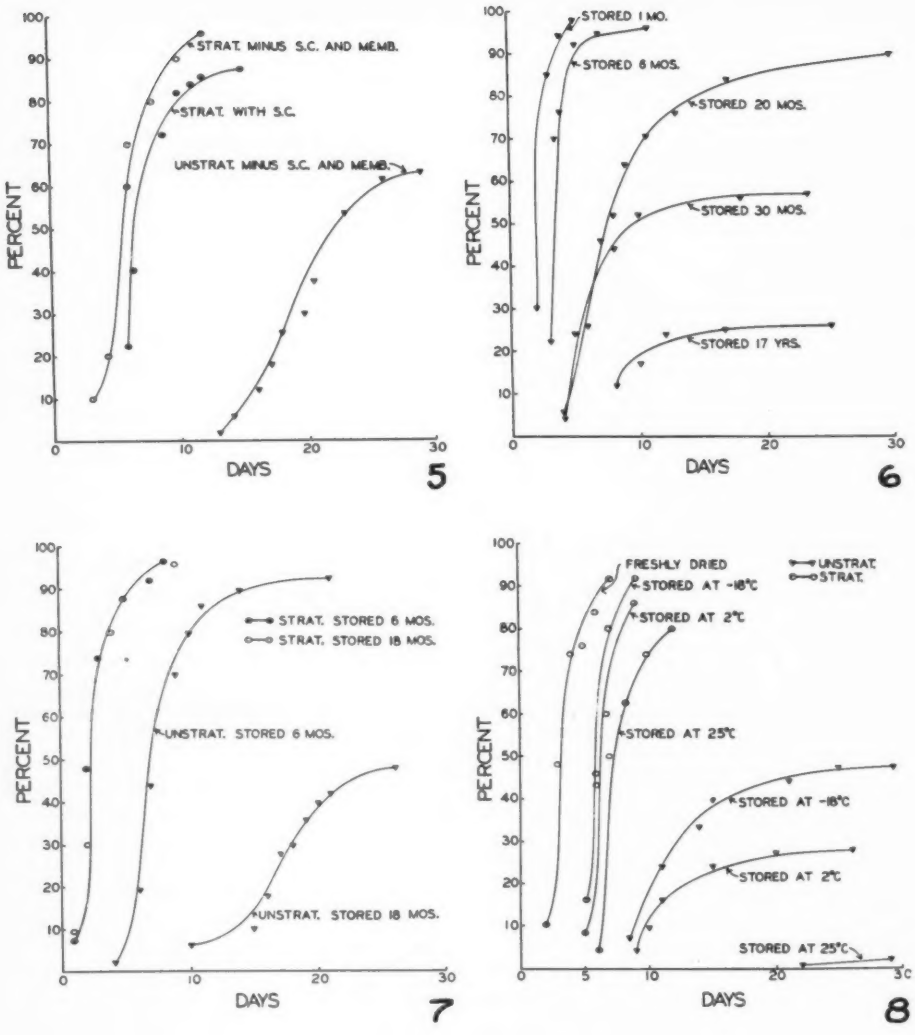


FIGURE 5. *Effect of seed coat and papery membrane on the germination at 10 °C. of stratified and unstratified seeds. (Seeds from lot 53 had been stored dry at 2° C. for 20 months prior to use.)* FIGURE 6. *Effect of dry storage at 2° C. on subsequent germination at 25° C. of unstratified seeds from which the seed coats and papery membranes had been removed. (Seed stored 17 years was from lot 36; all other seed was from lot 53.)* FIGURE 7. *Effect of dry storage at 2° C., on the subsequent germination at 15° C., of unstratified and stratified seeds from which the seed coats and papery membranes had been removed. (Seeds stored 6 months were from lot 53; those stored 18 months were from lot 48.)* FIGURE 8. *Effect of 30 months of dry storage at 3 different temperatures, on the subsequent germination at 10° C. of stratified and unstratified seeds from which the seed coats and papery membranes had been removed. (All seeds were from lot 53.)*

month-old seeds, in 10 days with 30-month-old seeds, and was never reached with 17-year-old seeds (differences all significant at the .05 level).

When the germination temperature was lowered to 15° C. the effect of storage was more pronounced (Fig. 7). Under this condition the 50-percent germination level was reached in 7 days with 6-month-old unstratified seeds, and in 27 days with 18-month-old unstratified seeds (differences significant at the .05 level). Again, as with intact seeds, the effect of storage disappeared after the seeds were stratified (Figs. 2, 7).

When the storage period was increased to 30 months, stratification no longer completely overcame the retarding effect of storage on germination (Fig. 8). Furthermore, the temperature at which the seeds were stored affected their subsequent germination. This was most clearly shown at lower germination temperatures when unstratified seeds, from which the seed coats and papery membranes had been removed, were used. It was also apparent when the seeds were stratified in addition to having the seed coats and papery membranes removed (Fig. 8).

Embryo vigor as measured by the elongation of the radicle and hypocotyl following germination. The number of seedlings that appear above ground in the nursery is not a measure of germination. Instead, it is a measure of the number of seeds that produce young seedlings after the seed has germinated and for that reason has been referred to appropriately enough as the "plant percent." Actually, three steps are involved: (a) germination, which is the earliest visible external manifestation of embryo growth, (b) elongation of the radicle after germination, and (c) hypocotyl elongation which in turn pushes the cotyledons above the surface of the ground. We have already seen how germination is affected by storage; now let us see how elongation of the radicle and the hypocotyl is affected.

Preliminary studies indicated that, once the seed had germinated, neither the presence nor the absence of the seed coat had any effect upon radicle or hypocotyl elongation. Therefore, since germination of unstratified seeds could be obtained within a few days by removing the seed coats and papery membranes (Figs. 4, 5), this technique was used in all subsequent studies including those reported here.

Radicle and hypocotyl elongation were studied at 25° C., 15° C., and 10° C. germination temperatures and the effect of storage was evident at all three levels. However, the effect of storage on subsequent radicle elongation was most pronounced at the 10° C. germination temperature. On the other hand, the effect of storage on hypocotyl elongation was best shown at 25° C. Therefore, to conserve space only data on radicle elongation at the 10° C. germination temperature and hypocotyl elongation at the 25° C. germination temperature are presented here.

Elongation of the radicle was affected by the seed storage period in much the same general manner that germination was affected. However, the storage period that could be overcome by stratification was much shorter, when measured by the number of seeds whose radicles reached 3 inches, than when measured by germination. As the storage period increased, the rate of radicle elongation as well as the number of germinated seeds whose radicles reached 3 inches decreased. Stratification completely overcame the retarding effect that short storage periods had on radicle elongation, but only partially overcame the retarding effect of longer storage periods (Fig. 9). For example, with stratified freshly dried seeds and stratified 6-month stored seeds germinated at 25° C., 95-percent of the radicles reached 3 inches, while with stratified 20-month stored seeds only 50-percent reached 3 inches (differences significant at the .05 level).

The storage temperature as well as length of storage had a pronounced effect upon radicle elongation (Fig. 10).

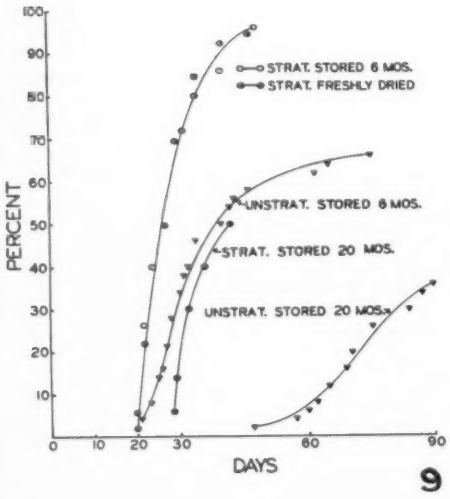
When stratified, 95-percent of the freshly dried seeds, 65-percent of the seeds stored for 30 months at −18° C., 50-percent of the seed stored for 30 months at 2° C., and 5-percent of the seeds stored for 30 months at 25°C. developed radicles that finally reached 3 inches when the seeds were germinated at 10° C. (differencs significant at the .05 level). When unstratified, less than 10-percent of the 30-month stored seeds developed 3-inch radicles, regardless of the storage temperature.

When germinated at 25° C. the hypocotyls of 90-percent of the seedlings from 6-month stored unstratified seeds reached 3 inches in 25 days (Fig. 11). When the seeds had been previously stratified the time required was reduced to 16 days which was the same as for stratified fresh seeds. When the seeds were stored for 30 months, stratification did not completely reverse the effect of storage even at the best storage temperature. For example, hypocotyl elongation of 75-percent of the seedlings from seeds stored at −18° C. reached 3 inches; when stored at 2° C., 45-percent reached 3 inches; and when stored at 25° C., 20-percent reached 3 inches (differences significant at the .05 level).

Discussions and Conclusions

At 25° C. embryo dormancy was not evident and fresh seeds germinated readily once the seed coats and papery membranes had been removed. On the other hand, when the temperature was lowered to 5° C. the embryo remained dormant until after a 3-month stratification period had passed.

Fresh seeds from a few cones closely fol-



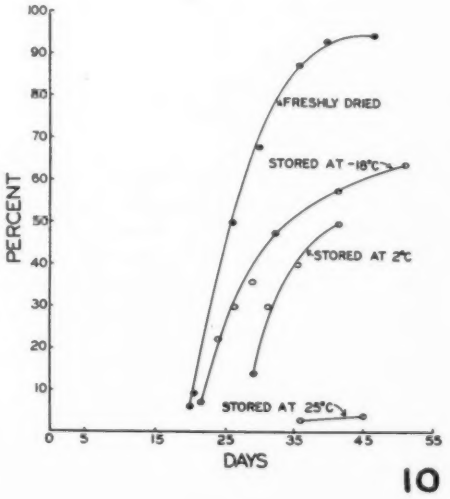


FIGURE 9. *Effect of dry storage at 2° C., on the number of days required for the radicle to reach 3 inches after germination at 10° C. Stratified and unstratified seeds were used from which the seed coats and papery membranes had been removed. (All seeds were from lot 53.)* FIGURE 10. *Effect of 30 months of dry storage at 3 different temperatures, on the number of days required for the radicle to reach 3 inches after germination at 10° C. Stratified seeds from which the seed coats and papery membranes had been removed were used. (All seeds were from lot 53.)*

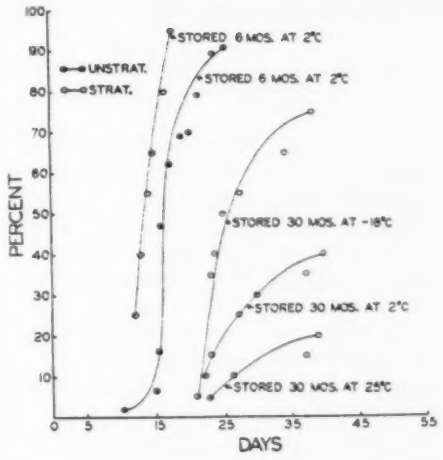


FIGURE 11. *Effect of dry storage at 3 different temperatures, on the number of days required for the hypocotyl to reach 3 inches after germination at 25° C. Stratified and unstratified seeds were used from which the seed coats and papery membranes had been removed. (All seeds were from lot 53.)*

lowed the *Pinus jeffreyi* seed germination pattern (Stone, 1957), whereas seeds from the large majority of the cones did not. However, when the seed coats and papery membranes were removed the cone differences disappeared and all the seeds behaved as did *Pinus jeffreyi* seeds when their seed coats and papery membranes were removed.

When the seed coats were left on, the germination behavior of *Pinus lambertiana* and *Pinus jeffreyi* became more and more alike as the temperature was lowered until at 5° C., where stratification occurred, their germination patterns became similar.

Thus we see that although *Pinus lambertiana* is a pine whose seeds are generally believed to require stratification and *Pinus jeffreyi* is a pine whose seeds are generally considered not to require stratification, there are many similarities in the germination behavior of the two, and that embryo dormancy in both seeds is a "relative" condition, becoming more and more pronounced as the germination temperature is lowered.

Without doubt, the use of the term "relative dormancy" will be questioned by some. Through general usage seed has been considred dormant when it fails to germinate under favorable conditions of moisture and temperature. For example, Crocker (1948) has stated that, "The main evidence that the embryos are non-dormant is the fact that conifer seeds in general will germinate and produce normal seedlings at 20° C. or above if given sufficient time . . . the time is likely to be rather long—more than 50 days for some species."

This interpretation is inconvenient and can be confusing if applied to *Pinus lambertiana* seed germination. After 3 months only a few whole unstratified seed will have germinated at 20° C., and none at 5° C. Furthermore, when the seed coat is removed the seed germinates readily at 20° C., but not at 5° C. However, when the seed has been previously stratified, it germinates readily at 5° C. regardless of whether or not the seed coat has been removed.

It might be argued that stratification involves a process of slow germination and that stratified seed is already partially germinated since, if held long enough at 5° C., it germinates—the "incipient germination" concept proposed by Mirov (1936a). However, the chemical changes occurring during stratification can also be obtained if moisture uptake by the seed is limited to an initial 48-hour period (Stone, 1957). Then the seed will not germinate regardless of how long it is held at 5° C. unless additional moisture is supplied.

This behavior is interpreted as evidence that the embryo of unstratified *Pinus lambertiana* seed is dormant at 5° C. and the embryo of stratified *Pinus lambertiana* seed is non-dormant at 5° C.

As reported earlier, the germination behavior of *Pinus jeffreyi* seeds at different temperatures as well as germination after the seed coats had been removed, suggested

that germination in pine seed involves a two step process and a working hypothesis was proposed (Stone, 1957). According to this proposal: (a) S→I→G, where "S" is the general substrate, "I" is one or more intermediate compounds, and "G" is growth, (b) at 5° C., the S→I step is more or less independent of the seed coat while the I→G step is retarded by its presence, and (c) at 15° C. and 25° C., the reverse is true with the S→I step being limited by the seed coat while the I→G step is more or less independent of the seed coat.

The germination behavior of both fresh and stored *Pinus lambertiana* seed lends support to this hypothesis. With stored seed, if it is assumed that the substrate "S" is gradually destroyed or in some other manner becomes unavailable as a result of prolonged storage, then smaller and smaller amounts of the intermediates "I" would accumulate during stratification. If it is further assumed that the elongation of the radicle is dependent upon the accumulation of "I," then its growth subsequent to germination should be proportional to the amount of "I" available. Finally, since germination only involves the initial few millimeters of radicle elongation, it should be less affected by a reduction in "I" than the subsequent elongation. Experimentally, stratification almost completely reversed the retarding effect which 30-month storage had on germination, but only partially reversed the retarding effect it had on the continued elongation of the radicle following its appearance at germination.

Pursuing this same line of reasoning, the higher the storage temperature the more rapid would be the reduction of available "S." This in turn should affect the subsequent elongation of the radical. Experimentally, after 30-month storage at 25° C. germination was still above 80 percent, but subsequent radicle elongation had been materially reduced and only 5-percent of the germinating seedlings developed radicles 3 inches or more in length. On the other hand, after storage at 2° C., 50 percent of the seedlings developed radicles 3 inches or more in length.

As suggested earlier, germination at 5° C. appeared to be dependent upon the slow accumulation of "I" while at 15° C. and 25° C. there appeared to be a fairly rapid production of "I," once the seed coat and papery membrane had been removed (Stone, 1957). If this is true, then as "S" disappears during storage, a point will finally be reached where, during germination, the amount of "I" accumulating at 5° C. will not be sufficient for full elongation of radicle and hypocotyl. Since "S" is apparently rapidly converted to "I" during germination at 25° C., there is no particular need for an accumulation of "I." Therefore, the effect of a reduction of "S" should show up first at the low germination temperature. Eventually, when "S" is still further reduced by continued storage, the effect should be apparent at 25° C. Experimentally, as the seeds aged, the number of seedlings that produced 3-inch radicles and 3-inch hypocotyls decreased more rapidly when the germination temperature was 10° C. than when it was 25° C.

Thus, the working hypothesis suggested for use in the continued investigation of the germinating mechanism of *Pinus jeffreyi* seed (Stone, 1957) appears to be equally useful in the investigation of the mechanism in *Pinus lambertiana* seed which deteriorates more rapidly during storage.

But of what practical value to the "forester" are the data given in this paper? First, the data presented should contribute to a better general understanding of seed behavior and should reduce the general confusion attendant on the question ". . . to stratify or not to stratify?" Second, it indicates the usefulness and limitation of the seed coat removal technique in germination tests of pine seed. Third, it indicates the variability in seed germination that can be expected with seed from different cones on the same tree. Fourth, and probably the most important, it indicates the danger of evaluating seed storage on the basis of a

simple germination test. This is particularly dangerous when the tested seed is to be used on a direct seeding operation. For example, fresh seed and seed stored for 30 months at −18° C. have an average germination of 95-percent (Figs. 8 and 9). Seed stored for 3 months at 25° C. has an average germination of 80-percent which is still considered good. However, only 5-percent of the seed stored at 25° C. produced a minimum 3 inches of radicle growth while 80-percent of the seed stored at −18° C. and 95-percent of the fresh seed did so. Consequently, had these three groups of seed been used for direct seeding, it is entirely possible that the seed stored at 25° C. and even some of that stored at −18° C. would have been unable to send down a radicle sufficiently long to escape desiccation when the top few inches of soil dried out in the spring.

Thus, before the "forester" buys x pounds of seed at y dollars a pound and plants this seed at z dollars an acre, he should determine the expected average embryo vigor as well as the expected average germination.

Summary

1. The germination behavior of *Pinus lambertiana* seeds depended upon: (1) the particular cone they came from, (2) the length of time they had been stored, and (3) the storage temperature.

2. At 25° C. most intact seeds germinated slowly or not at all and in this respect differed from *Pinus jeffreyi* whose intact seeds germinated rapidly at this temperature. However, when the seed coats and papery membranes were removed the germination behavior of the two species was essentially the same.

3. At 25° C. embryo dormancy was not evident, but when the temperature was lowered to 5° C. the embryo remained dormant until a 3-month stratification period had passed. This was interpreted as it was in an earlier paper on *Pinus jeffreyi*, as a condition of "relative" embryo dormancy. Justification of this interpretation is also presented.

4. Radicle and hypocotyl elongation following germination was used as a measure of embryo vigor. Vigor was unaffected by the presence or absence of the seed coat, but was affected by the length of time the seed had been stored as well as the storage temperature.

5. Embryo vigor of fresh seeds was not materially affected by stratification. On the other hand, embryo vigor of stored seeds, which was low, was improved by stratification.

6. Embryo vigor was best maintained at a storage temperature of −18° C.

7. Seeds stored at 25° C. for 30 months germinated slowly, even when the seed coats and papery membranes had been removed. After stratification these same seeds germinated rapidly. However, the embryo vigor of these seed, although improved by stratification, was still unsatisfactory.

8. Germination behavior of *Pinus lambertiana* seeds supports the hypothesis, suggested in an earlier paper, that a two-step chemical process is involved in the germination of pine seed. Specifically, the reduction in the germination capacity as well as the subsequent radicle and hypocotyl elongation following prolonged storage, suggests that a metabolic substrate is reduced during storage and gradually becomes limiting.

9. Practical implications of this research are discussed.

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The Climate near the Ground

By Rudolf Geiger. A translation by Milroy N. Stewart and others of the second German edition of Das Klima der Bodennahen Luftschicht with revisions and enlargements by the author. Second printing, revised. Blue Hill Meteorological Observatory, Harvard Univ. Press, Cambridge, Mass. 494 pp. illus. 1957. $6.00.
Review by Ashbel F. Hough

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Field men in forestry often experience rigorous climatic conditions. They and other outdoorsmen realize that the microclimate or climate near the ground is even more erratic and subject to greater extremes than the regional climatic averages indicate. Those of us in the modified climate of large cities, living in air conditioned offices and homes, conveyed in heated or air conditioned vehicles powered by fossil fuels, and wearing clothing adapted by experience and research for protection from heat and cold, are less aware of local microclimatic factors.

Since all humanity is dependent on the green plant directly or indirectly for food and other materials necessary to sustain life, the influence of microclimate or the "plant climate" on crops, forage, and forests, affects us far beyond our personal comfort alone. To quote from Geiger's classic book ". . . all plants have their lives conditioned by that very zone of disturbance which had been so meticulously avoided in meteorological observations."

The vagaries of the climate near the ground were known to the ancients but systematic observations were not made, or basic principles developed, until the early part of the twentieth century. Pioneers were Gregor Kraus who published in 1911 in Germany and H. J. Cox who reported experiments on cranberry culture in Wisconsin in 1910. Rudolf Geiger, now teaching at the University of Munich, and his pupils, have contributed much to the basic science of microclimatology and to its practical applications.

Foresters in particular owe a debt of gratitude to Geiger for his scholarly review, evaluation and presentation in book form of a vast number of literature references. Much of his work was done in the field of forest meteorology.

The first edition in German appeared 30 years ago, the second edition in 1941 and the third in 1950. Word of the third edition reached the United States while a translation of the second German edition was being prepared. With the author's cooperation the first English edition was supplemented with additions which made the translation the virtual equivalent of the third German edition. The present or 1957 book is a second printing of the 1950 text with a revision of the bibliographic material and correction of a few errors.

Despite the lack of a critical review of recent English literature in the field of microclimatology, Geiger's book, translated in 1950, still stands as a basically sound and readable text. The student and practicing forester can gain both theoretical background and much of practical application. The illustrations are good but require conversion of metric and centigrade units to English equivalents. The approximately 500 references added to the 1957 printing have been separated from those referred to in the text and designated "Supplementary Bibliography," pp. 445-472. Arrangement is by chapter headings as with the text references. Failure to include certain references listed in the earlier 1950 printing somewhat reduces the value of the supplementary list.

The flood of scientific literature makes it difficult for even the specialist to keep up with the times. Whether one should purchase this book for the list of supplementary references alone is a question of personal choice and interest in the field. Nothing new is added to the text though this is probably the publisher's rather than the author's fault and stems in part from translation expense had Geiger been asked to make a fourth German revision.

Shelterbelts and Microclimate

By J. M. Caborn, Dept. of Forestry, Edinburgh University, Forestry Commission Bulletin No. 29, 135 pp. 1957. price 17s. 6d. net.

Review by Ralph A. Read
Rocky Mountain Forest and Range Experiment Station, U. S. Forest Service, Lincoln, Nebraska

In this complete treatment of the rather specialized subject of windbreak influences, Maurice Caborn has done forestry, and in particular Plains forestry, a real service. For quite a number of years, research on the influence of windbreaks upon the microclimate of adjacent agricultural fields and range lands, has lagged in the United States. The classic work of Carlos G. Bates[1] has long been out of print, and to some extent lost to those working in Plains forestry. Caborn brings this important work back to life in his excellent review of the literature.

The bulletin is divided into three parts: 1. An extensive review of the literature which covers nearly one-third of the paper; 2. A critical survey of research procedure, including previous experimental methods and instrumentation, and possible new developments for future studies; 3. A description and results of experimental work undertaken by the author, chiefly with models in the wind-tunnel. There are 28 plates showing instruments, wind-tunnel models, and typical field windbreaks tested in Britain. There are over 200 references including significant papers by world-wide authorities in the field of windbreak research. It would have been helpful to use English titles, as well as the foreign titles in the literature references.

In reviewing past work, Caborn first discusses the influence of windbreaks on air flow considering penetrability, height, and width of barrier as affecting the sheltered area. Next, he discusses the other factors of environment separately and as modified by wind movement; these are temperature, humidity, evaporation, soil moisture, precipitation, and snow distribution. These are each discussed in relation to the way they are affected by windbarriers, and compared to open field conditions. The rather brief discussion of the economic significance of

[1] Bates, Carlos G. Windbreaks: their influences and value. U. S. Forest Service Bull. 86, 1911. 100 pp.

environmental modification caused by windbreaks is undoubtedly due to the paucity of research data on this subject and consequent lack of published results in terms of crop or animal yields and their conversion to monetary values. Caborn states, "That a definite increase in agricultural productivity in areas sheltered by tree belts is to be expected, more than adequately compensating for the loss of the area occupied by the shelterbelts or the narrow zone which may be sterilized by their roots and overshading, has been firmly established in principle" (page 32). This may be, as far as windbreak foresters are concerned, but it is little recognized by most agricultural people in the Great Plains, possibly because the influences of windbreaks on crop yields have not been studied by agronomists.

Previous studies and abundant observational evidence have shown that tree plantings can be useful as tools of farm and ranch management in dry, windy, agricultural areas. Therefore, the study of influences and the economics of windbreaks for protection to soils, crops, and livestock should be an important phase of agricultural research. This stands in contrast to the other major phase of windbreak research which deals with the problems of establishing, maintaining, and protecting the tree plantings. While the later phase is unquestionably the job of the forester, or whatever you wish to call the Plains tree planter, the former involves many agricultural skills, including those of the agronomist, agricultural economist, engineer, meteorologist, animal husbandman, and soil scientist.

Caborn stresses that further field investigations are desirable to substantiate present evidence and to translate results of wind-tunnel studies into field research. We might add that much of this research might be done by agronomists and agricultural economists, who may be better qualified than most foresters to evaluate treatment effects on agricultural lands.

For those agricultural workers interested in knowing of the possibilities for modifying field microclimate for the growing of crops and animals, Caborn's bulletin is highly recommended. All windbreak foresters should own a copy.

Economics of Plantations

By W. E. Hiley, Faber and Faber Ltd., London, 216 pp. 25s.

Review by Kenneth P. Davis
The University of Michigan, Ann Arbor.

As with Mr. Hiley's preceding volume *Woodland Management*, this book is specifically British in its setting and purpose. But as always when a subject is thoroughly probed, there is much of value in it to anyone concerned with the subject material. It is written by a man with long and deep forestry experience. Earlier a teacher, he has for many years been a forest manager with the necessity for careful business management to show a profit.

Prior to about 1920, British forests were almost entirely of hardwoods very irregular in size and quality. In more recent years many and large plantations of conifers have been planted and are beginning to yield commercial products in quantity. A new forest industry is developing as a result of great need to grow more timber in Britain.

It is estimated that Britain can supply about one-third of its needs, and as Mr. Hiley emphasizes, it should grow what can best compete with imports. Choice of species, the size and kind of products grown, and utilization equipment employed, all should be gauged

from this standpoint.

The costs and returns of plantation establishment, care, and ultimate harvest are the center of interest in this book. The point of view is essentially an area, a plantation as a unit. Regulated "going concern" enterprises are few though the author points out and demonstrates that a going concern situation in nowise invalidates financial analyses of individual tracts.

This book is basically built around calculation soil expectation values, using the Faustmann formula, as Mr. Hiley prefers to designate it. To this reviewer, it would seem preferable to place less emphasis on formulas and names as the process is no single or proprietary affair. The concepts of soil rent and forest rent have been argued at length and with some confusion. Terminology can obscure the basic problem which is the application of discount to the costs and returns of growing timber as Mr. Hiley ably demonstrates.

A wealth of background and specific information on costs and returns for British plantation forestry are given. Problems of cost accounting and of yield estimation using existing yield tables are frankly and fully faced. A series of representative, experience-based cost and return data are developed which form the basis for financial analysis of plantation management.

The real meat of the book is the treatment of how to apply these data to thinning practice. Mr. Hiley's major thesis, developed at length, is that early and heavy thinnings, "may reduce the cost of growing timber trees by as much as 50 per cent and even more." Emphasis is placed on major harvest yield although intermediate yields are fully considered. He develops calculated yield tables based on heavier and different thinning schedules than are incorporated in existing British and German published yield tables. The process of developing these new tables will be of much interest to American foresters. Hiley seems particularly critical of German low thinning applied to British conditions.

Thorough analysis is given of the effect of growth rate, the timing of production costs and of income on financial returns. The Faustmann formula approach is applied in several ways:

1. To solve for the length of rotation using an assumed interest rate and schedule of costs and returns.
2. To reverse the process and determine the rate of return for different rotation either with no assumed land value (the usual Se calculation) or with different assumed land values applicable when land is bought to begin with.
3. To study the effect of interest rate on different cost components.
4. To determine what price must be received to yield a given rate.
5. To determine the increased cost per inch of diameter as the rotation is lengthened.

The book gives a sharp and realistic analysis of comparative valuation applied to plantation management. In some respects there seems undue preoccupation with compounding of interest at the expense of broader economic analysis. Not all financial calculations and valid economic objectives can or need be handled through the Faustmann formula approach. Mr. Hiley writes clearly and directly but some calculations are hard to follow without considerable background in this kind of analysis and an understanding of British conditions and terminology.

The Effects of Defoliation by the Lodgepole Needle Miner

BY
R. W. STARK
J. A. COOK

AN OUTBREAK of the lodgepole needle miner, *Recurvaria starki* Free[1], has persisted in western Canadian National Parks for more than a decade. Investigations of sampling procedures, biology and ecology have been published but there has been no critical report of the damage caused to trees. Thus far in Canada this damage has not been of economic importance but examinations by R. W. Stark have shown that needle miner outbreaks in California can cause death of trees (Figs. 1 and 2). Patterson (1921) describes some of the earlier infestations of the lodgepole needle miner in Yosemite National Park, Calif., in which many trees were killed, resulting in ghost forests. It was believed for many years that the needle miner merely weakened the trees, making them susceptible to bark beetle attack, particularly by the mountain pine beetle, *Dendroctonus monticolae* Hopk. There has been no evidence in the Canadian outbreak that bark beetle populations have increased and there is ample evidence in the current infestation in Yosemite National Park that the needle miner alone has killed large numbers of trees.

The main value of the lodgepole stands in the area affected by the Canadian outbreak is to provide forest cover on an extensive watershed. The distribution of the needle miner includes Jasper and Banff National Parks which contain the headwaters of the Saskatchewan River system, and Yoho and Kootenay Parks which contribute to the Columbia River system. Aesthetic value must also be considered since the affected stands are entirely within national parks.

Although it will be shown in this paper that there is no immediate danger to these stands, an estimate of the damage incurred during the outbreak is necessary. More important, however, is the development of criteria for assessing and predicting possible future damage. The results presented here are based on more or less continuous studies from 1948 to 1955. The extensive raw data and analyses are available in the Annual Technical Reports of the Division of Forest Biology, Calgary Laboratory, for the years 1949 (Graham and Stark);

[1] The lodgepole needle miner in the Canadian outbreak has been described by Dr. T. N. Freeman of the Entomology Division, Ottawa, as *Recurvaria starki* (Pan-Pacific Entomologist, 33:1, Jan. 1957). Publications concerning this insect prior to 1952 referred to it as *Recurvaria milleri* Busck; following 1952, as *Recurvaria* Sp.

Contribution No. 333 from Forest Biology Division, Science Service, Department of Agriculture, Ottawa, Canada. The authors are stationed at the Forest Biology Laboratory, Calgary, Alberta.

FIGURE 1. *Defoliation and shortening of needles caused by the lodgepole needle miner,* Recurvaria milleri *Busck. in Yosemite National Park, Calif.* FIGURE 2. *"Ghost" forests resulting from past outbreaks of the lodgepole needle miner in California.*

1950, 1951 and 1952 (Stark); 1953, 1954 and 1955 (Stark and Cook).

Estimation of Defoliation

Life history of the insect. The life history of the California species was described by Patterson (1921), and that of the Canadian species by Stark (1954a). A brief comparison of the two species was made by McLeod (1951).

The life cycle of this species occurring in Canada covers approximately 24 months, of which 21 are spent in the larval stages. Adults normally appear in the even-numbered years, for example, 1952 and 1954. Moth emergence begins the first week in July and is generally completed by the first week in August. Egg laying is completed by late August. Larvae only are present from this time until early summer of the next even-numbered year. Pupation begins early in June of the next even-numbered year and is usually completed by June 30.

The larva begins to mine a needle soon after emerging from the egg; the majority prefer the younger needles. Unless the population is extremely heavy, only one of the two needles in a bundle is mined. The unattacked needle in the bundle is not affected by the mining of the other, an important fact in the assessment of defoliation. The first needle mined is usually completely hollowed out by July of the odd-numbered year when the larva is about one year old. At this time the larva transfers to a second needle. Younger needles are preferred but needles of almost any age may be attacked. By late October this needle is from half to three-quarters mined and the characteristic yellow of the mined needle is noticeable. The second needle is completely mined by the middle of May of the following year. The larva then transfers to a third needle which it mines completely before pupation in June. The outbreak is most noticeable at this time. The mined needles of the 3 years are present on the tree; the first 2 years' needles have darkened to a reddish brown; the last year's are still bright yellow. This imparts a yellowish-red tinge to the forest.

Methods of determining defoliation. Defoliation estimates were made in 1949 following the pattern set for needle-miner population sampling (Stark, 1952a). A branch tip bearing the last five years' needles was accepted as a sampling unit. This was chosen because the proportion of insects mining needles older than five years was negligible. From the standpoint of defoliation, it has been observed that the proportion of needles older than five years remaining on the branches is very low when compared with the whole tree crown.

In determining defoliation, all the needles on a sample tip were counted and classified as green, mined, or dead from other causes. The number of missing needles was determined by counting bundle scars, care being taken to omit flower scars. All missing needles were attributed to defoliation by the needle miner. In 1949, 96 tips were examined in this manner. These were taken from 4 areas, 8 tips from each of 3 trees. Four tips each were taken from the upper and lower parts of the crown and the defoliation of the two crown levels was compared. Samples from the mid-crown gave an acceptable average for the total crown (Stark, 1952a). The areas sampled were:

1. Yoho National Park at valley bottom plus 300 ft. or 4,800 ft. above sea level (a.s.l.) in the vicinity of the Spiral Tunnels of the Canadian Pacific Railway.
2. Lake Louise in Banff National Park at valley bottom (5,100 ft. a.s.l.)
3. Mount Eisenhower, Banff National Park at valley bottom (4,800 ft. a.s.l.).
4. Mount Eisenhower, 700 ft. above valley bottom (5,500 ft. a.s.l.).

The two areas at Mount Eisenhower became particularly interesting following an extremely severe winter in 1949-50. In the valley bottom, the infestation was practically wiped out, whereas at elevations 500 ft. or more above the valley bottom the

infestation declined gradually from 1950 to 1956.

Population counts, including mortality estimates, were made annually in each area. Simple mathematical methods were applied to assess defoliation using the 1949 figures as a basis. The number of needles added annually to each branch tip was assumed to be constant.

In 1954, five trees were selected on Mount Eisenhower at an elevation of 5,500 ft. Sixty branch tips from each tree were taken at mid-crown and examined in the same way as in 1949. Defoliation was calculated on the basis of the total number of needles normally present compared with those actually present and not mined. All missing needles were attributed to defoliation by the needle miner, which in effect would tend toward an over-estimation of damage by the insect. This is considered preferable to possible under-estimation and simplifies calculations. The defoliation calculated for this area in 1954 was compared with that predicted for the same period by extrapolation from the 1949 defoliation data and yearly population estimates. All four areas have been computed to the current year, 1955, on the same basis.

The investigations discussed above pertain largely to mature and overmature trees. In 1950 Graham and Shepherd (1951) established a relationship between tree height and number of branch tips using trees in the vicinity of Mount Eisenhower. This makes it possible to establish, with due consideration for differences in stand density, the number of branch tips from a height measurement, and hence a measure of total defoliation from population estimates.

Results and discussion. The basic data necessary for computing defoliation are presented in summary form. These include:

1. Population and mortality estimates for each year or major stage in the life cycle. This implies double sampling during the moth-flight year as the tips are, in effect, attacked twice, first by the survivors of one generation and second by the progeny of these survivors. However, one sampling would suffice in the odd-numbered year when larvae only are present. The survivors of the first winter plus the dead larvae would constitute the beginning population of that generation.
2. The number of needles present on the tip at the start of the estimate and the number added yearly.
3. An estimate of the defoliation at the beginning of the study.

Table 1 shows the distribution of the needle miner over the sample tip. This information is descriptive in value as it illustrates the course of defoliation for two different years. The computation is simply subtractive by deducting the total number of needles mined each year from the total number present, in the last five years' growth. In both instances, as clearly verified by the weighted average of the 2 samples, three-quarters of the attack was in the first 3 years' needles of a branch tip.

The needle complement of a mature pine (80 to 100 years old) was calculated for each area. The average number of needles produced yearly for the period 1945-49 was found to be 65 (standard error = 5). In 1954 the average for the period 1950-54 was 77 (standard error = 5). The inter-tree variability encompassed a range of means from 67 to 96 per year, while the

TABLE 1. Proportion of needle miner attack in each year's needles.

Age of Needles	Proportion of Attack[1] 1949	1954	Weighted Ave.
1	.32	.11	.16
2	.21	.27	.26
3	.25	.34	.32
4	.15	.17	.16
5	.07	.11	.10

[1]Basis: 96 tips in 1949 and 300 in 1954.

intra-tree variability, the year-to-year variation based on the average for five years, ranged from 59 to 89 per year.

It is realized that in addition to a large inherent variation in the number of needles produced each year there may be other factors influencing needle production, of which tree age is perhaps the most important. Also, it has been observed that needle production on heavily-flowering branches or trees is less than where flowering is absent or light. All counts were made on non-flowering trees. No significant difference was found between yearly needle production from 1950 to 1954 in the Mount Eisenhower area. The 1949 data were not extensive enough to determine yearly differences.

For a technique of this sort it would be overly precise to attempt to determine the number added each successive year for the estimation of defoliation. Therefore, a weighted average was calculated and 75 taken as the yearly increment and 375 needles per tip as the "normal" number of needles for both actual and theoretical defoliation calculations, a revision resulting from the 1954 data.

Yearly population estimates are required to estimate the progress of defoliation. Although comprehensive records on all of the areas were not kept for the full period (1949-1955), from data available it was possible to reconstruct a reasonably precise population history (Table 2). The application of these data to cumulative defoliation analysis is presented for one area only, the highest area on Mount Eisenhower, because the check in 1954 permits an estimation of the accuracy of the procedure (Table 3). Some explanation of how the estimated defoliation given in this table is calculated may be helpful. The number of green needles in 1949 is the starting point and is the first row in the table. The assumption is then made that 75 needles per tip are added yearly. This is based on a weighted average of many counts. Now, for example, consider the 5 figures in the first row under 1945-1949. If there were 75 needles per year added, then there should be a total of 375 present. But in row 1, there are only 166 present ($26 + 19 + 32 + 30 + 59$). Defoliation is attributed to needle miner and thus:

$$\frac{375\text{-}166}{375} \times 100 = 56 \text{ percent.}$$

A similar calculation has been made for

TABLE 2. Needle miner population history pertinent to defoliation estimates, 1950-1955.

Time of population estimate[1]	Area and elevation: Yoho 4800 ft.	Lake Louise 5100 ft.	Mount Eisenhower 4800 ft.	Mount Eisenhower 5400 ft.
	Number live larvae per tip			
Spring, 1950	21	2	< 1	4
Fall, 1950	31	20	< 1	25
1951	26	6	< 1	20
Spring, 1952	20	5	< 1	16
Fall, 1952	22	13	6	27
1953	21	12	5	26
Spring, 1954	10	< 1	< 1	14
Fall, 1954	10	5	1	11
1955	2	1	1	4

[1]The dotted line indicates successive generations of the insect.

TABLE 3. Estimated defoliation from population counts Mount Eisenhower, 5500 feet, 1949-1955.

Number of green needles present by years											Estimated percent defoliation
1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	
26[1]	19	32	30	59							56
(Spring)	19	32	30	55	75						
(Fall)	16	28	22	49	71						50
		26	19	42	66	72					40
		(Spring)	17	36	61	69	75				
		(Fall)	15	33	54	64	72				37
				32	51	58	68	72			26
				(Spring)	50	54	65	70	75		
				(Fall)	49	52	61	67	74		19
					28	36	46	57	73[1]		36[2]
						35	45	55	72[1]	74	25

[1]Actual count.
[2]Actual percent defoliation.

other periods and the percent defoliation is shown in the last column. The number of needles present for each succeeding year is calculated by subtracting the number of needles which would be mined by the population for that year from those found in the first count (first row). Defoliation is estimated only for the fall. The green needles present in 1954, again by actual count, are shown in the next to the last row. Thus the figure of 36 percent defoliation is actual rather than estimated.

The estimated defoliation on each of the four areas sampled continuously since 1949 is presented in Figure 3. The revised figures for Mt. Eisenhower, altitude 5,500 ft., are also plotted.

Defoliation in the Mount Eisenhower stands in 1954 ranged from a low of 27 per cent to a high of 43 per cent with an average of 36 per cent. The estimated defoliation based on the 1949 sampling was 20 per cent for the fall of 1954. Comparing the actual number of green needles present in 1954 with those estimated (Table 3) it can be seen that the error increases as the needles become older. As the current year's foliage in 1954 was 73 needles, this error cannot be entirely due to over-estimation of needles added yearly. From this it appears that natural needle drop may be a larger factor than originally supposed but the error is not large enough to warrant attempts to refine the

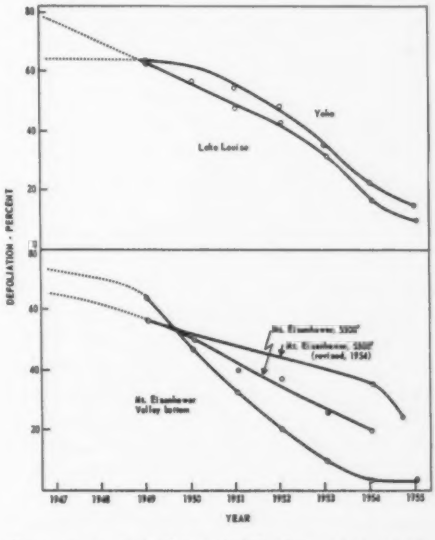


FIGURE 3. *Calculated defoliation, 1949-1955, of lodgepole pine stands in four areas.*

technique any further. Also, it must be remembered that this accounts for only the defoliation caused by the needle miner and not by other defoliating insects such as budworm and sawflies, nor defoliating pathogens such as needle casts, all of which occur to some extent in these areas. However, as detailed tip examinations are made each year, such increases would be detected and could readily be incorporated in the analyses. A portion of the error is a result of population sampling but this can be calculated (Stark, 1952, a, b).

The decrease in defoliation since 1949 in all areas sampled (Fig. 3) is a reflection of decreasing needle miner populations. It is evident, however, that peak populations occurred sometime prior to 1949. From a consideration of tree mortality and the rapid recovery of current foliage complement in less than a decade, it was postulated that the outbreak started early in the 1930's and reached its peak between 1940 and 1944. Records from 1948 indicate that the number of live larvae per tip was as high as 87 with an average of about 30 in the heavier areas, Mount Eisenhower and Lake Louise. The number of larvae per branch tip at the peak of the outbreak must have been from 60 to 75 at the valley bottom and from 45 to 50 at the higher elevations to cause the defoliation recorded on the various areas in 1949. Hopping (1945 a) reported the percentage of mined needles in 1944. These were based on 33 branch tips bearing needles of the last 2 years and the population was approximately 31 larvae per tip. Converting these to equivalent five-year tips by Table 1 gives an estimated population for the spring of 1944 of about 65 larvae per tip. In 1945, by the same sampling method, the population was approximately equivalent to 44 per five-year tip (Hopping, 1945 b), indicating that the outbreak was beginning to decline at that time. By inference, the population in the fall of 1942, the beginning of the generation which was sampled in July of 1944, must have been considerably larger than 65 per tip. If these infestations had persisted, mortality of trees would almost certainly have occurred by 1960. Many of the trees in the Lake Louise area, where they are mature to overmature (100 to 200 years) survived only because of the rapid decline in populations. The older trees were left with only tufts of foliage at the tops of the trees.

The curve for the 5,500 ft. elevation on Mount Eisenhower is particularly significant. This shows, but to a lesser degree, the same general decline as the three valley bottom areas. It has been established in past studies that intensity of needle-miner attack usually decreases with altitude so this is to be expected (Stark, 1952 a). However, with the winter conditions of 1949-50, it was demonstrated that in the Bow Valley trench at least, the middle slopes (approximately between 5,000 and 6,000 ft.) constitute a "refuge" area for the needle miner as there was greatest survival at these elevations (Henson, et al, 1954). The defoliation curve supports these findings. The population at the 5,500 ft. elevation declined as did the others after 1948 but did not suffer the catastrophic mortality that occurred in the valley bottom at Lake Louise and Mount Eisenhower. Hence the defoliation curve for this area shows a steady decline rather than the abrupt drop which occurred in the valley bottoms. A high mortality in 1954-55 is reflected in a rapid decrease in the Yoho area as well.

The comparison of the defoliation estimates with the check of 1954 and with the theoretical defoliation curves presented in the next section shows that the technique of combining population estimates with defoliation estimates has a practical predictive value within reasonable limits of accuracy.

Prediction of Defoliation Using Population Estimates

In the previous section actual population counts were used to estimate current defoliation. The next step, therefore, was to draw up theoretical defoliation curves from which it would be possible to estimate future defoliation, mortality of trees, and if possi-

ble the expected time to tree mortality. The utmost value of such curves would be realized if they could be used from a single measurement, which could be easily obtained. This can be done by using the sequential sampling technique for determining the current larval population and expressing the defoliation expected in terms of the number of live larvae per tip.

Population sampling method. Sequential sampling provides a rapid technique for survey use. When originally derived, three arbitrary classes of severity of infestation were used (Stark, 1952 b). The present study indicated more useful limits based on actual defoliation and the limits were revised accordingly (Stark, 1954 b). The defoliation expected has been changed slightly, otherwise the classes presented in Table 4 are the same as in the previous publication.

It must be emphasized that the 10 per cent accuracy given by this sampling system applies only with respect to the 4 classes. For example, one can be sure he is within 10 per cent accuracy that a given population is medium-heavy *within the definition for that class* but the actual population may lie anywhere between 30 per tip and 50 per tip. For use with the predictive defoliation curves in the next section, a precise population count is required only for the "heavy" class, as populations below 50 per tip will probably never cause tree mortality. If the populations are greater than 55 per tip, a more intensive sample is necessary.

Methods for prediction of defoliation. The needle data presented in the previous section were used to establish theoretical defoliation curves. Seventy-five needles added yearly was assumed to be constant, making a total of 375 needles in the sample tip. The distribution of the assumed attack was taken from Table 1.

The cumulative defoliation percentages were estimated for six assumed intensities of attack: 20; 40; 60; 70; 80 and 100 larvae per tip. It was further assumed that these were the population levels at the beginning of each life cycle of the insect. It can be seen at once that the year and time of year the samples are taken are important in interpreting the effect of the population from the defoliation curves. The only time the sample will not necessarily be followed by a reduction in number is in the spring of the moth flight year. The number of larvae attacking the foliage in the fall may be much larger than the number of survivors of the previous generation.

TABLE 4. Revised sequential sampling classes related to defoliation, 1954.

Live Larvae per tip	Classification	Expected defoliation
Number		*Percent*
<5	Light	<10
>10 but <25	Medium-low	>10 but <25
>30 but <50	Medium-high	>20 but <50
>55	Heavy	>50

Beginning with the assumed intensities of attack on the full needle complement at the beginning of a generation of the insect, two mortality constants were applied. These were not completely arbitrary but were based on the average of all mortality in all areas since 1948. The extremely heavy mortalities in some areas in 1949-50 and 1954-55 were excluded, because they constituted special cases.

The first mortality constant, 20 per cent of the total population, was applied against the starting population in the spring of the odd year, after the larva had mined its first needle. This constant represents winter mortality and is indicative of the actual mortality. In past studies, there has been no measurable larval mortality prior to the first winter hibernation nor during the first summer's larval stages.

The second mortality constant, 25 per cent, was applied in the spring of the next even year, after the larva had mined its second needle and generally before the third. This is deducted from the remaining population. Of the 25 per cent, about 20 per

cent of this mortality is caused by climatic factors, 5 per cent by parasites and other causes. Actually, total parasitism of the needle miner population has averaged about 15 per cent but the majority of the parasitized larvae mine their third needle before succumbing. For the study of defoliation therefore, they are essentially "alive."

The calculations involved in estimating defoliation are the same as those presented in Table 3. The assumed intensities of attack are distributed over the branch tip according to the data of Table 1 and the mined needles subtracted according to the assumed population. The mortality constants are applied as indicated above. It is obvious that neither the beginning populations nor the mortality factors remain constant and this must be taken into account for a true appraisal.

Results and discussion. The theoretical defoliation curves based on six assumed intensities of attack are presented in Figure 4. An example of the use of the chart will serve as explanation.

Suppose the needle miner population was sampled in mid-summer of 1955 by the sequential sampling system and the cumulative count of live larvae per tip for 100 tips was found to be 7,500 or 75 per tip. According to the sequential classification the population is "heavy" and expected defoliation is greater than 50 percent (Table 4).

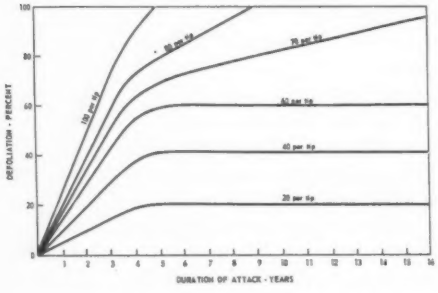


FIGURE 4. *Theoretical defoliation of lodgepole pine with different assumed intensities of needle miner attack.*

Referring to the defoliation chart (Fig. 4), a population of 75 per tip, beginning from a nil attack, would achieve 100 percent defoliation in approximately 13 years. If the assumed attack had increased to 75 per tip from 60 per tip the tree already would have been about 60 per cent defoliated and 100 per cent defoliation would then be achieved in approximately eight years *if the population of 75 per tip remained constant for that period.*

A comparison of the end points of the actual defoliation curves in Figure 3 (the population estimates of 1955) and theoretical curves (Fig. 4) will give some indication of their usefulness and accuracy.

In Yoho, the population in 1955 was found to be 2 per tip. From Figure 4, neglecting past history, the defoliation should be less than 5 per cent. From Figure 3 it can be seen that current defoliation is 15 per cent, a difference of about 10 per cent. The trend of the curve is towards the lower level.

At Lake Louise, the 1955 population was about 1 per tip, hence the defoliation should be much less than 5 per cent. The calculated defoliation (Fig. 3) is about 10 per cent. This curve trend is also toward a lower level and should the needle miner population remain low, we can expect that the trees in the Lake Louise area will regain their normal needle complement.

Trees in the valley bottom, at Mount Eisenhower, show no visible evidence of insect damage after 5 years of low needle miner populations. From Figure 3 the calculated defoliation is about 3 per cent. This estimate conforms to what is expected from the low insect populations.

The use of the curves at attack intensities which would cause tree mortality could not be checked in Canada as the population was never high enough or sustained long enough. However, in Yosemite National Park, Calif., where a severe needle miner attack occurred, rough comparisons by R. W. Stark indicated that the curves would probably yield the expected results.

The technique as described herein provides a rapid means of classifying an outbreak of the lodgepole needle miner from an economic viewpoint. The population samples which are the basis of the technique are rapidly and easily obtained, using the sequential sampling method. These figures are related to the curves which give the defoliation expected if the population has not been unusually larger or smaller in the immediate past and if it remains constant. The value of this procedure is obvious where control of any sort is contemplated. Priority can be ascribed to areas on a temporal basis, because it can be determined where and approximately when tree mortality will occur.

Growth Studies

Effects of defoliation on needle growth. From counts made in 1949 and again in 1954 there is no conclusive evidence that the actual number of needles produced each year was reduced by defoliation of the needle miner. Nor was there significant evidence that this occurred in the California outbreak. Visual observations by G. R. Hopping of the Calgary Laboratory prior to 1948[2] and by R. W. Stark in 1948 and 1949 while the outbreak was still at a high level, indicated a shortening of the needles. This was markedly evident in the California trees where repeated defoliation had removed all but the current year's foliage (Fig. 1, inset).

Lateral-terminal growth reduction. Early in the summer of 1953 the damage index developed by Benjamin et al (1953) for red pine was investigated as a possible index for needle miner damage. In this method, the correlation between ratios of lateral to terminal elongation was used as a criterion for evaluation of the effects of spittlebug injury.

The technique was tested in the Rocky Mountain region in unattacked lodgepole pine and in three intensities of attack by the lodgepole needle miner. Terminal and lateral measurements were taken from a total of 100 trees representing six areas and three age classes. However, the technique was found inapplicable. It is perhaps of little importance to speculate why it does not apply but it is probably related to the difference in the type of feeding of the two insects. Needle miner damage is general, scattered throughout the crown and on all branches and the injury should result in reduction in all growth functions of the tree such as shortening of needles, reduction in lateral, terminal, and ring growth. The spittlebug attack is confined to individual branches, causing a reduction in growth or death of branches which was reflected in the change of the lateral-terminal growth ratio for that year (Benjamin et al, 1953).

The data collected were compared using standard statistical techniques. It was found that there was a significant reduction of both lateral and terminal growth in attacked trees. The data are presented for two age classes in Table 5. It is obvious that a significant reduction in both lateral and terminal growth has occurred in young trees with defoliation of about 40 per cent. When the Yoho trees are compared with those from Johnson's Canyon and Kananaskis, defoliation of approximately 10 per cent apparently did not have this effect.

Similar results are evident for the 60-80 year class. In the older trees measurements were taken of branch and terminal growth back to 1947. The reduction was also apparent at that time. The estimated defoliation in 1953 was considerably less than had occurred in the past. An apparent recovery of growth has taken place and as populations have continued to decline, this apparent recovery can be studied further.

The reduction in terminal and lateral growth of young and mature lodgepole pine resulting from defoliation by the lodgepole needle miner is apparently dependent upon the degree of defoliation.

[2]Personal communication from G. R. Hopping, Forest Zoology Laboratory, Calgary, Alberta, 1955.

TABLE 5. Lateral-terminal growth reduction in lodgepole pine due to needle miner defoliation.

Area	Age of trees	Estimated Defoliation (1953)	Year	Terminal Growth[1] Mean	Terminal Growth[1] S.Ex	Lateral Growth[2] Mean	Lateral Growth[2] S.Ex
	Years	*Percent*		*cm.*		*cm.*	
Yoho (1)	10-15	40	1953	31.8	2.03	12.13	0.50
			1952	28.0	2.03	10.20	0.48
			1951	29.0	1.44	10.50	0.37
Yoho (2)	10-15	40	1953	28.8	2.51	10.12	0.52
			1952	24.8	2.09	9.03	0.39
			1951	26.8	2.43	9.50	0.40
Johnson's Canyon	10-15	10	1953	44.4	2.33	17.70	0.67
			1952	36.0	0.92	14.28	0.52
			1951	33.8	1.57	14.13	0.31
Kananaskis	10-15	0	1953	46.6	1.47	16.07	0.75
			1952	40.1	1.88	14.70	0.57
			1951	38.7	1.14	14.19	0.52
Mt. Eisenhower 4900′	60-80	15 (over 60 in 1949)	1953	9.4	1.03	3.17	0.22
			1952	6.6	0.73	2.90	0.14
			1951	9.4	0.79	4.67	0.18
Mt. Eisenhower 5500′	60-80	45 (up to 60 in 1949)	1953	3.0	0.51	1.83	0.14
			1952	3.8	0.63	2.05	0.13
			1951	5.3	0.63	3.13	0.14
Yoho	60-80	35 (over 60 in 1949)	1953	9.3	0.96	5.94	0.26
			1952	7.9	0.72	4.83	0.23
			1951	8.2	0.71	5.69	0.22
Two-Jack Lake	60-80	Nil	1953	24.5	1.28	9.80	0.31
			1952	21.3	0.65	8.82	0.30
			1951	25.4	0.83	10.17	0.37

[1]Each sample of 10 trees.
[2]All branches (5) in each whorl of ten trees sampled.

Development of a Technique for Analysis of Increment

Introduction. The effect on radial increment resulting from defoliation by the needle miner has been determined for young lodgepole pine. This effect was resolved by the use of a new approach to the study of tree growth presented by Duff and Nolan (1953). They demonstrated graphically that external factors influencing growth of red pine, *P. resinosa* Ait., could be clearly delineated by eliminating the inherent growth factor referred to as "pattern." This is defined by Duff and Nolan as: "systematic factors or complexes of factors, the operation of which result in a certain uniformity or pattern in the distribution of growth activity no matter what the circumstances of growth may be . . ." These factors are believed to be intrinsic

in nature.

The first application of Duff and Nolan's techniques in this study was to young lodgepole pine and the investigation was extended to determine its applicability for growth analysis of mature trees. The original procedures are lengthy and time consuming, making large-scale analysis impractical. A method to surmount this objection was developed, whereby the essential analytic concepts were retained, but sampling was greatly reduced.

The growth sequences proposed by Duff and Nolan were used in their original form, but the brief, descriptive names proposed by Mott[3] were used for discussion purposes. The sequences are illustrated in Figure 5 and are defined by Duff and Nolan as follows (Mott's terminology in parentheses):

Type 1 (oblique) sequence. "Strong, regular pattern of gradually rising, maximating, and falling mean, internodal ring width of a single year's growth, with progression from internode to internode down the tree. Progression in space is both radial and longitudinal. There is no progression in time of origin of the rings, which are contemporaneous. But the succession of internodal cambia from which the rings are formed are of progressively increasing age. Randomly distributed variations are present but only as a superimposition upon and therefore dominated by the regular variations of the pattern."

Type 2 (radial) sequence. "Strong, regular pattern of gradually rising, maximating, and falling mean, internodal ring width in a single internode with progression from one ring to the next. Progression in space is radial only. Progression in time does not involve change from the product of one internodal cambium to that of another, but does not entail progressively increasing age of the single internodal cambium. Randomly distributed variations present, but again superimposed upon and dominated by systematic variations of the pattern."

Type 3 (vertical) sequence. "Essentially unpatterned variation of mean, internodal ring width with progression from internode to internode down the tree at a uniform ring number from the pith. Progression in space is longitudinal only and is devoid of radial component. All the rings of a given sequence were laid down in their respective internodes when those internodes and cambia were a uniform age. Thus the progression in time does not involve cambial age but does involve the formation of the successive rings of the sequence in successive years which involves apical activity. Randomly distributed variations are clearly manifest and are not dominated by systematic, patterned variations in this type of sequence."

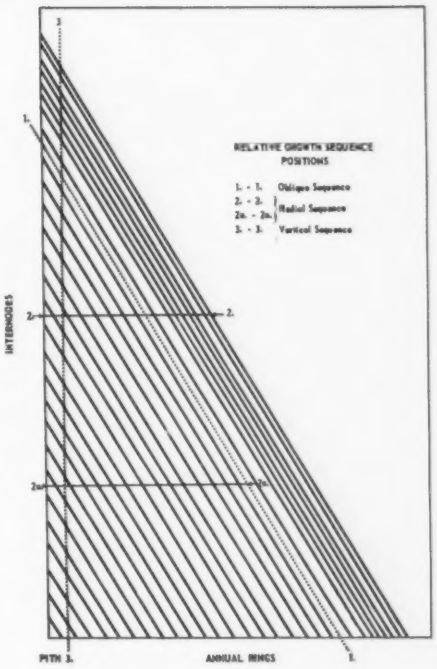


FIGURE 5. *Schematic diagram of tree stem showing position of growth sequences.*

Growth sequence analysis of mature trees. In order to demonstrate the applicability of the study techniques mentioned above to mature trees, it was necessary to compare some growth influence common to both

[3]Mott, D. G., L. D. Nairn, and J. A. Cook. Radial growth in forest trees and effects of insect defoliation. For. Sci. 3:286-304. 1957.

TABLE 6. Characteristics of two trees and their sites for growth sequence comparison.

Characteristic	Mature tree	Young tree
Age (years)	110	33
Height (feet)	65	32
Stand density	very dense	open-grown
Moisture relations	cool and moist	warm and dry
Slope	flat	steep
Elevation (feet a.s.l.)	3800	4100
Aspect	N. E.	S. W.
Macroclimate	— — — common — — —	

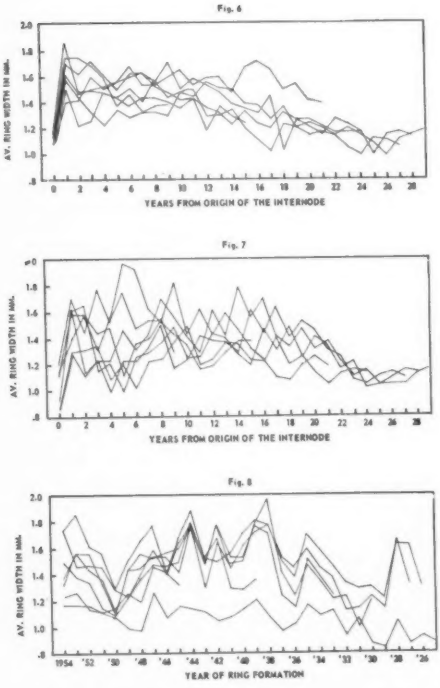


Fig. 6
AV. RING WIDTH IN MM.
YEARS FROM ORIGIN OF THE INTERNODE
Fig. 7
AV. RING WIDTH IN MM.
YEARS FROM ORIGIN OF THE INTERNODE
Fig. 8
AV. RING WIDTH IN MM.
YEAR OF RING FORMATION

FIGURES 6 to 8. *Growth sequences for a 30-year period from an unattacked mature tree, Ottertail Creek, Yoho National Park. Fig. 6—oblique. Fig. 7—radial. Fig. 8—vertical.*

young and old age groups by means of these techniques. Two trees were selected for comparison from the Kickinghorse Valley of Yoho National Park, 6 miles south of Ottertail Creek. The characteristics of the trees and their respective sites are summarized in Table 6. The trees were chosen less than one-quarter mile apart, in an area which has been free of insect outbreaks for at least a decade. From Table 6 it can be seen that, as far as possible, all factors affecting growth except macroclimate are different. This factor should then be dominant in expressing differences by this method of analysis. The reaction of the trees to this common external influence should be similar for the comparable growth periods. If their reaction for this 30-odd year interval is similar, then it should follow that the growth of the mature tree in its entirety, could be analyzed by the same techniques as used for the young tree.

The tree was sectioned in each of the last 30 internodes. These sections were taken at a point two-thirds of the internodal length below each node. The average width of each ring was calculated from the mean of 4 radii on each disc and then plotted according to the oblique, radial and vertical growth sequences (Figs. 5 to 11). The graphs were simplified by using only 10 of the 30 sequences sampled in each tree. Figure 12 shows the average vertical sequence for each tree.

The oblique and radial sequences of both trees illustrate the effect known as pattern (Figs. 6, 7, 9, 10). There is the characteristic sharp rise, maximation, and then gradual decline of the conventional growth curve trend. The effect is more pronounced in the young tree than in the top portion of the mature tree. This is a reflection of the relative growth vigor of the trees, but the pattern effect is very evident, though differing in amplitude.

The vertical sequences for both trees show definite similarity in their general trend or "configuration." Configuration is defined by Duff and Nolan as: Systematic factors or complexes operating to induce

regularity in the distribution of growth activity which, however, is not the same under all circumstances but varies with variation in such conditions as site and stand density." Pattern is absent and the configuration in both trees is similar (Figs. 8 and 11). The irregularities in both trees agree remarkably, showing comparable oscillations, although varying in magnitude, in 22 out of 27 points. This can only be the result of a major common extrinsic growth influence.

The tree and site characteristics presented in Table 6 show that macroclimate is probably the only major extrinsic factor common to both trees. Its effects are modified by the individual tree sites, but in each case the main growth trend for each tree is the same. The combined effect of all the factors on growth is reflected in the differences in amplitude of the corresponding points on the two curves (Fig. 12).

This almost complete agreement in growth trend indicates that the older tree reacts in a like manner to the younger tree. The overall trends for each tree, for all sequences, adhere to the principles proposed and developed by Duff and Nolan in their study of growth in young red pine. We may therefore assume that this method of growth analysis is applicable to lodgepole pine, irrespective of age, site or density factors.

Short-cut sampling technique for growth analysis. In 1953, six mature trees from the Lake Louise area were examined by the methods described above. These trees were from an area heavily infested by the needle miner. The purpose was to demonstrate that growth reduction could be resolved with a simpler sampling and analytic method. The vertical sequence was used for separating external growth influences such as insect attack from inherent growth characteristics.

Five discs were taken at evenly spaced intervals from each tree. From the top disc, ring measurements were made from the 1953 ring back to the ring formed in 1927. The set of rings measured in the second disc were the same age from the pith as the first set, but were not of the same temporal age. The 3 lower discs were measured in the same way. These measurements are illustrated in Figure 13 where each curve represents the mean radial growth for the 5 levels. The year of formation of the last ring plotted is shown for each of 5 age levels in the tree. Each of these last rings, however, is the fortieth ring counting out from the pith. Thus the conditions of vertical arrangement required

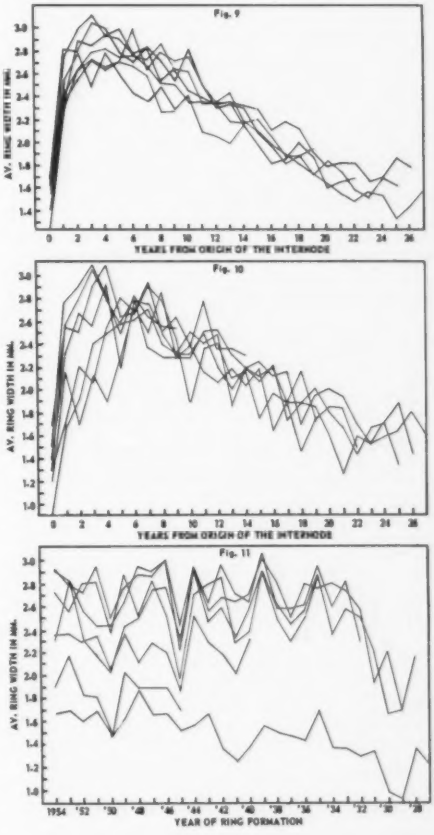


Fig. 9
AV. RING WIDTH IN MM.
YEARS FROM ORIGIN OF THE INTERNODE
Fig. 10
AV. RING WIDTH IN MM.
YEARS FROM ORIGIN OF THE INTERNODE
Fig. 11
AV. RING WIDTH IN MM.
YEAR OF RING FORMATION

FIGURES 9 to 11. *Growth sequences for young unattacked tree for a 30-year period, Ottertail Creek. Fig. 9—oblique. Fig. 10—radial. Fig. 11—vertical.*

by the analyses are fulfilled on the ordinates. If the curve points at each ordinate are plotted, a series of vertical growth sequences would result, each consisting of five points. The curves in Figure 13 were smoothed to clarify the trend.

Curves 2 to 5, in general, parallel one another, particularly when two adjacent discs are compared. All of these rings were formed prior to the needle miner outbreak, curve 2 ending just about the time of the outbreak peak. Curve 1 parallels curve 2 very closely until approximately 1938, when a radical departure begins, coinciding with the estimated period when defoliation reached damaging proportions. The percentage reduction for the entire infestation period could be ascertained by computing the area differences under the curves, allowing for the average normal separation in the left-hand portion of the curves prior to the defoliation effect.

The parallelism in almost all adjacent disc curves, and particularly in the first portions of curves 1 and 2, suggests that if the needle miner infestation had not occurred, curve 1 would have continued to parallel curve 2. If this supposition is true then a two-level sample of radial measurement would provide a reasonably accurate determination for the date of initial increment reduction and a measure of total growth loss for the attack period. One disc should include the period of insect attack and a corresponding period prior to attack, the other a period of comparable age, ending just prior to the insect attack so there is an overlapping of ring ages. This was the final sample decided upon. The disc including the attack period is referred to as the "damage" curve, the other as the "base" curve. The relative positions of these curves are shown diagrammatically in Figure 5: 2a—2a representing the base curve; 2—2 the damage curve.

Testing the short-cut technique. To insure that the sampling system described above depicted a true effect of external growth factors, it was deemed advisable to test it further. For this purpose data from 2 trees at Ottertail Creek (Figs. 8 and 11) and a third young unattacked tree from Kootenay Park were used. The sequences for these 3 trees from unattacked areas are compared on the 2-level basis with sequences of two other heavily infested young trees, one from Vermilion Pass, one from Lake Louise, and with the curves from Figure 13 for an overmature tree from Lake Louise (Figs. 14 to 19). The dam-

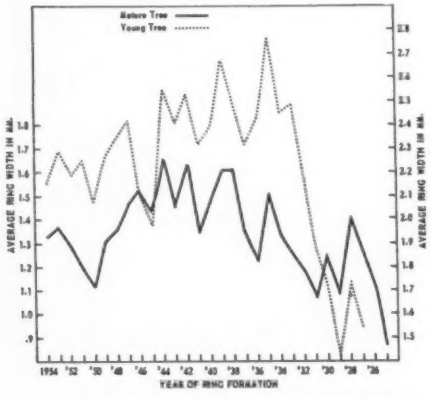


FIGURE 12. *Average vertical sequence for a 30-year period for trees from Ottertail Creek.*

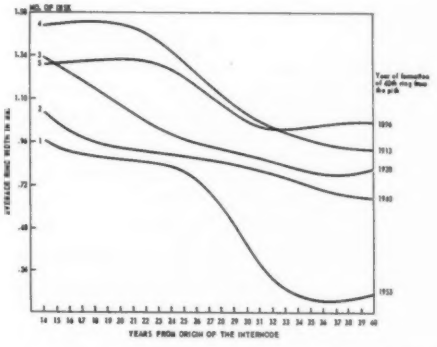
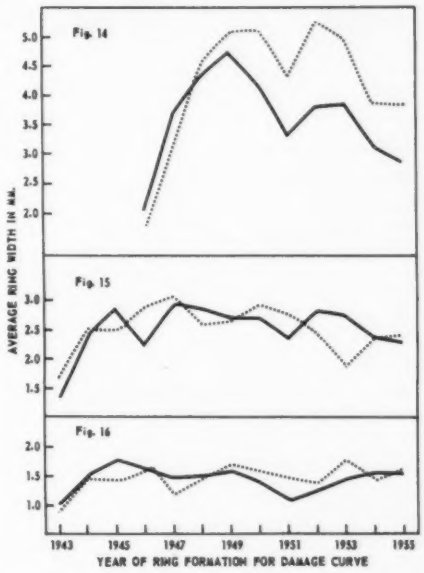
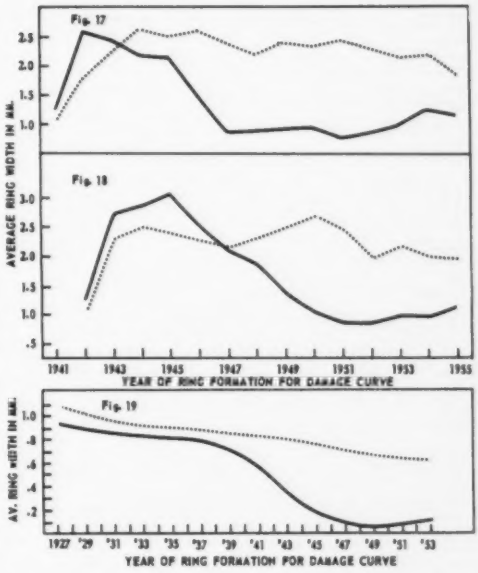


FIGURE 13. *Average radial sequence at five levels for six mature, heavily attacked trees from Lake Louise, Banff National Park.*



FIGURES 14 to 16. *Average two-level radial sequence curves for unattacked trees from three areas: Fig. 14 Kootenay Park 30 years old. Fig. 15 Ottertail Creek 30 years old. Fig. 16 Ottertail Creek 110 years old. Damage curve solid line, base curve dotted.*



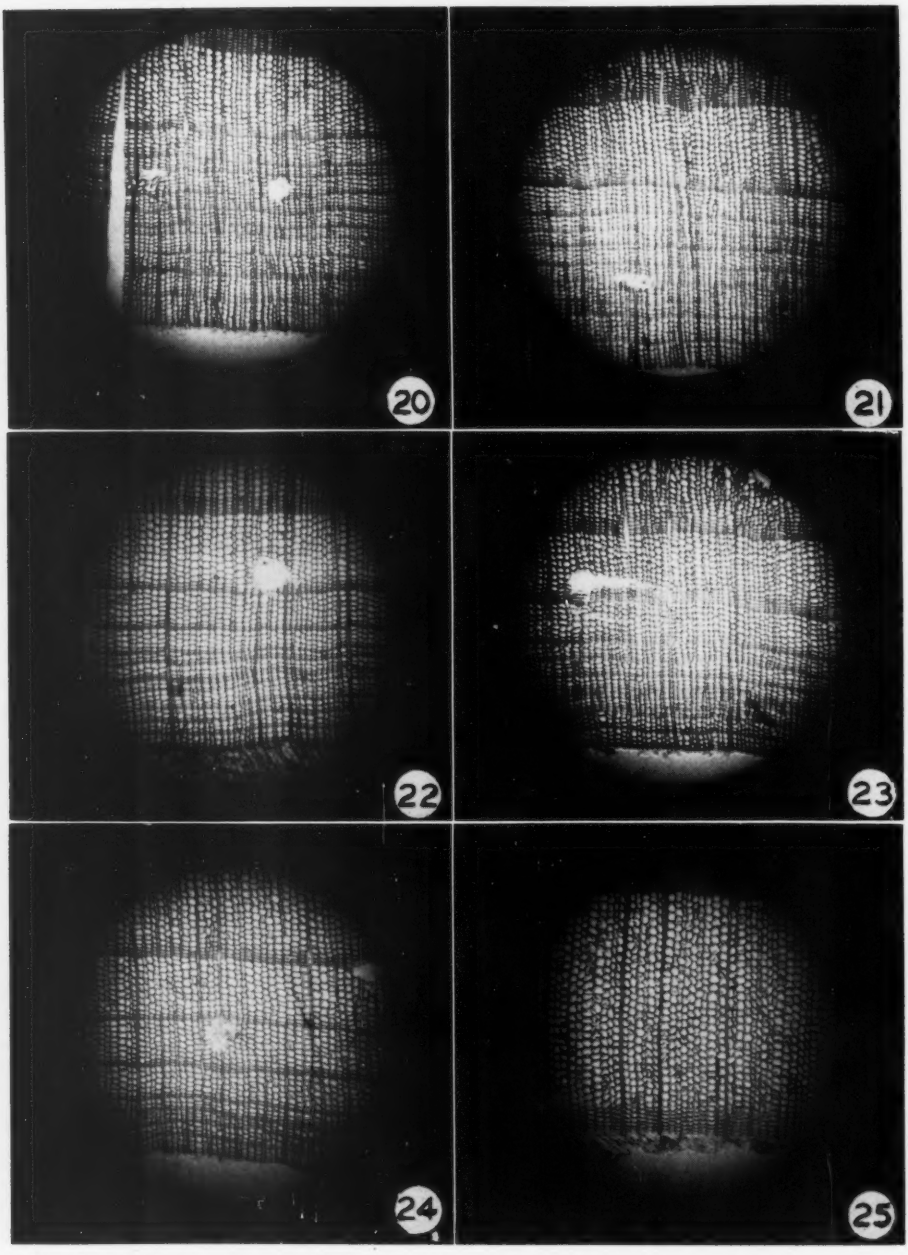
FIGURES 17 to 19. *Average two-level radial sequences for attacked trees from two areas: Fig. 17, Lake Louise 40 years old, defoliation about 60 percent. Fig. 18, Vermilion Pass, Banff Park, 30 years old, defoliation about 60 percent. Fig. 19, Lake Louise, 110 years old, defoliation 75 percent.*

age curves are drawn as solid lines, the base curves dotted.

The sets of curves for the unattacked trees show clearly that, barring the major external influence of an insect attack, the damage curve parallels the base curve. This fact is emphasized by the distinct separation of the curves in the infested trees: The individual curves are not of the same amplitude (Fig. 14), nor is this to be expected as long as the growth trends are approximately parallel. The portions of curves of the infested trees prior to the attack period illustrate this point. The dates of divergence in all cases (Figs. 17, 18 and 19) correspond closely with estimated defoliations approaching the 50 per cent point. There is evidently a time lag of about 2 years after sufficient defoliation has occurred before a reduction in increment becomes apparent.

This comparison of attacked and unattacked trees by the two-level sampling system yields the information required in such damage studies. The attack dates determined by this method agree closely with those estimated from population studies and defoliation analyses.

Defoliation estimates further substantiate the deduction that lessened increment in lodgepole pine probably does not occur until defoliation approaches 50 per cent in young trees and about 40 per cent in mature trees. According to Benjamin (1955) defoliation of about 50 per cent in jack pine is required before there is any noticeable loss in increment. Burger (1950) states that 50 per cent reduction in crown



FIGURES 20 to 25. *Cross-sections of part of the outer rings of the tree stem at five successive levels down a tree heavily infested by needle miner from 1940-44 (20-24). Fig. 25 shows a typical year's growth of an unattacked tree for 1953 (×60).*

volume is required in young pines before increment is reduced. The reductions shown in Figures 17 to 19 agree with these observations.

Variations of increment reduction within the tree. Figures 20 to 25 present photomicrographs showing the reduction in radial increment in a mature tree from Lake Louise. In addition to the two-year lag in increment reduction referred to before the results of defoliation become evident, there is a lag between the time this reduction appears in the upper bole of the tree and in the lower part (Figs. 20 to 24). The lag is almost equal to half the heavy attack period. Similar results were found in spruce by Swaine and Craighead (1924) and Reeks and Barter (1951) following attacks by the spruce budworm.

This effect should be taken into consideration when samples for the measurements of the two growth curves are being taken. For maximum efficiency they should be taken as far up the bole as is practicable considering the period of time over which the factor being studied has been in operation. That is, it would be impossible to achieve the coverage required for a 10-year outbreak unless the sampling extended downward to a point where 30 rings were present.

Application of the short-cut technique to lodgepole pine in Yosemite National Park, California. The lodgepole pine in this area is undergoing heavy attack by a needle miner which is similar to the Canadian species in many respects, particularly in its feeding behavior. Discs were procured from trees in two areas a few hundred yards apart where the attack varied from very heavy to light. The defoliation in the former was estimated at about 80 per cent, that in the light area at less than 30 per cent.

Growth analyzed by the methods discussed above is presented in Figures 26 and 27. The heavily attacked trees show a distinct curve separation commencing about 1943. The heavy attack was noted first about 1945 but was probably building up prior to this time.[4] The lightly attacked tree shows a growth reduction starting in 1947 and decreasing strongly to 1949, indicating a heavier population in years prior to this. In 1949 a very heavy spray was applied to this local area. The subsequent years show a rapid growth recovery to 1951, then the growth curves return to a parallel trend. During these last 5 years, the defoliation by the needle miner has been in the neighborhood of 30 per cent. The growth recovery under this population condition indicates further that the lodgepole pine can withstand defoliation up to 30 per cent without growth reduction.

Tree Mortality

Mortality of lodgepole pine is expected when complete defoliation occurs. Craighead (1940), reporting on experiments in the artificial defoliation of jack pine and scotch pine, both comparable to lodgepole pine, found that death resulted when trees were completely defoliated at any time of the year. Removal of the current year's foliage after it had developed resulted in the death of jack pine but some scotch pine survived. Removal of old foliage did not cause any mortality, even when repeated for three years. These observations were supported by Busgen and Munch as reported by Church (1949), who found that artificial defoliation of several young pines at different times of the year caused death in all instances, but there was variation in the time between defoliation and death. Burke as reported by Church (1949) found that stripping of lodgepole pine by coincident attacks of the lodgepole needle miner and a sawfly caused the death of the trees that season. Benjamin (1955) in intensive investigations on the red-headed pine sawfly, found that in the Northern United States and Canada jack pine succumbs to a single complete defoliation.

[4]Struble, G. R. Private communication. Calif. For. and Range Expt. Sta., Aug. 31, 1955.

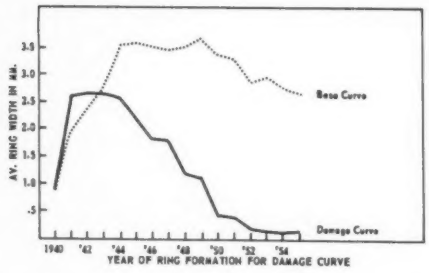


FIGURE 26. *Two-level growth sequences of lodgepole pine, heavily attacked by needle miner from Yosemite National Park, Calif.*

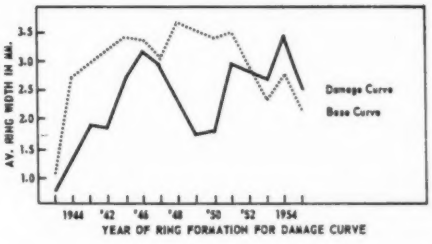


FIGURE 27. *Two-level growth sequences of lightly attacked lodgepole pine, Yosemite National Park, California.*

A survey to determine actual tree mortality was undertaken on 8 areas within the Canadian outbreak. At intervals of one chain, random samples of 25 trees were examined. Trees with any green foliage whatever were classed as alive. A total of 200 trees was examined for each area and on the slopes between Lake Louise and Louise Junction, where the heaviest defoliation occurred, 400 trees were checked. There was an extremely low mortality of trees in the "heavy" attack areas and none in most of the others (Table 7). Most of the dead trees were suppressed and probably would have been shaded out in any event. In no case were the dominant trees attacked by bark beetles in sufficient numbers to cause death; in fact, the evidence of bark beetles was negligible. From this survey it was evident that the outbreak did not persist at attacks over 60-70 larvae per tip for a period long enough to cause tree mortality. However, on the basis of investigations since 1948, tree mortality would probably have occurred within a decade or about 1960, particularly in the Lake Louise area, if the infestation had persisted at the levels present immediately prior to 1948.

TABLE 7. Tree mortality caused by the lodgepole needle miner, 1953.

Sample Area	No. trees checked	No. dead trees	Percent mortality
Lake Louise B.N.P.	400	15	3.5
Eisenhower, valley bottom B.N.P.	200	0	0
Eisenhower, 5,376′ B.N.P.	200	2	1.0
Baker Creek B.N.P.	200	0	0
Cascade Valley, B.N.P.	200	0	0
Wapta Lake, Y.N.P.	200	1	0.5
Hawk Creek, K.N.P.	200	0	0
Snow Creek, K.N.P.	200	0	0

Summary

1. The lodgepole needle miner caused as much as 80 per cent defoliation of lodgepole pine in Banff National Park, Canada, but defoliation never, except in a few over-mature trees, reached 100 per cent. The greatest defoliation probably occurred from 1940 to 1944. Since 1945 there has been a decrease varying in location with differences in needle miner populations, until at the present time (1956) maximum defoliation in any part of the outbreak is not above 40 per cent. Had the outbreak continued at levels present from 1940 to 1944, mortality of trees would have occurred, probably by 1960.
2. A method is presented whereby from population estimates obtained by survey sampling it is possible to estimate within 10 to 20 per cent, the percentage defoliation, expected tree mortality, and approximate time to expect tree mortality. The use of such a method in

control or management requires a knowledge of the main features of the life history of the insect and the sampling technique. Past history of defoliation can be deduced from the condition of the trees and the future defoliation estimated by the application of this method.

3. Terminal and lateral growth were significantly reduced by a defoliation of 40 per cent with negligible reduction at 10 per cent.
4. The study of growth analysis by the methods of Duff and Nolan (1953), already known to apply to young lodgepole pine, were also found to be applicable to mature trees of this species.
5. A sampling and analytical technique using two discs was developed which retained the vertical sequence of Duff and Nolan as the means for separating external growth influences. This materially reduces the labor involved while still retaining the ability to delineate the time an increment reducing agent came into effect and the probable magnitude of the effect. The magnitude can be determined by measuring the separation of the two curves, which should remain parallel, assuming no abnormal external growth influence such as insect attack was operative. One curve is referred to as the "damage" curve and covers the period of insect attack and a corresponding period prior to insect attack. The second, or "base" curve covers an equivalent period ending just prior to the effect of insect attack. Thus, the two curves overlap for approximately half the study period, establishing the normal relationship.
6. Analysis of many discs clearly showed a lag in effect of defoliation on increment between the upper and lower bole. For accurate determinations, using the sampling technique described, samples should be taken from the portion of the bole within the crown.

Acknowledgments

In a study which has covered a period as long as this, it is impossible to extend acknowledgments to all who contributed. Particular thanks are due G. R. Hopping, Officer-in-Charge of the Laboratory of Forest Biology, for his constructive criticism and guidance throughout the course of the work and in the preparation of the manuscript. Associates at the Calgary Laboratory have all contributed through discussions and observations and to them also we owe our thanks. G. R. Struble, of the California Forest and Range Experiment Station, Berkeley, Calif., assisted in the observations made on the California outbreak.

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